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# BOTANICAL GAZETTE

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## RELATION OF SOIL MOISTURE TO DESERT VEGETATION[1]

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(WITH FOUR FIGURES)

INTRODUCTION.—Of a number of lines of study now in progress, looking toward some quantitative knowledge of the relation obtaining between vegetation and environmental conditions, the determination of the march of soil moisture at Tucson has now progressed sufficiently far to warrant publication. The present paper deals with a continuation of the data upon soil moisture published by the writer under the title: "The soils of the Desert Laboratory domain" in SPALDING'S recent monograph on desert ecology (1). The data there presented comprise observations on soil moisture content extending over the period from October 1907 to April 1908. The period of observation has now been extended to March 1909, thus including both the spring dry season and that of the summer rains. To make the present presentation complete, the observations already published are here included.

RELATION OF SOIL MOISTURE TO OTHER FACTORS.—Just as the evaporating power of the air and the nature of the transpiring organs practically determine the water requirement of plants, so do the soil moisture content and the nature of the root system determine the water supply. Aside from those cases (of toxic soils and soils of high osmotic pressure) where the nature and amount of the solutes in the soil solution exert an influence upon the character of the root system or upon the rate of water absorption

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by these organs, and aside from those cases where the chemical content of the atmosphere or the character or intensity of illumination exert an influence upon the structure of the transpiring organs or upon the general tone of the plant, the simple relation between soil moisture and the evaporating power of the air appears to be of prime importance in determining the character of the natural vegetation. Over an area such as that here considered, where the air and light conditions are approximately uniform, and where the chemical content of the soil appears not to vary sufficiently to produce variations in plant growth, the possible rate of water supply to plant roots may be supposed to become the limiting condition. This rate of supply depends primarily upon the absolute amount of soil moisture and upon the water-conducting power of the soil.

Soil moisture, of course, depends upon the rate of influx and the rate of removal of water from the soil. The former is determined by the ability of the soil to raise water from the subterranean water table, where such exists, by the amount and time of precipitation or other water entering the soil from above or laterally, and by the water-retaining power of the soil. Water removal from the soil is a resultant of evaporation at the soil surface, downward movement into lower layers, and plant absorption.

Throughout the area here studied precipitation is approximately uniform. Surface drainage, nearly uniform within the extent of each soil type, is quite different (because of variations in slope and porosity) for the four types. The water-retaining powers of the four soils are also different. Underground drainage is very different for the different soils, as is also the depth of permanent subterranean water, which is practically quite absent from two of the soils.

THE SOIL TYPES.—The geology and topography of the Tumamoc area are thoroughly described by TOLMAN in the monograph of SPALDING above cited. Tumamoc Hill, on which the Desert Laboratory stands, rises abruptly from the broad valley of the Santa Cruz River. The valley floor slopes very gently from the base of the hill to the river floodplain and to the various "washes," tributaries of the main river channel. The four soils here considered

may be briefly described as follows. A more complete description is included in the author's article above cited.

1. The soil of Tumamoc Hill is a heavy clay, underlaid by practically impervious rock at a depth of but 10–50 cm., and much broken into small pockets and irregular masses by outcropping rock or large rock fragments. Fully 50 per cent of the entire gross volume of the soil is made up of large and small rock masses. A subterranean water table does not exist here, so far as is known, and, from the impermeability of the underlying rock both to water and to plant roots, it is safe to conclude that the water supply for this soil is derived exclusively from precipitation. The unsifted soil possesses a water-holding power of 48 per cent of its dry weight. The usually pronounced slope of the soil surface here is partially offset by the numerous small catchbasins formed by rock fragments, so that rain water stands in small pools over the hill and does not drain away quite so rapidly as though the surface were more even.

2. The soil of the *Larrea* slope, so named from the prevalence of the creosote bush thereon, occupies the gentle slope which surrounds the hill. This soil is underlaid at a depth of 20–30 cm. by the limestone hardpan (caliche) so common in this region. The surface soil is more loamy than that of the hill, with an admixture of about half its volume of fine angular gravel; that near the caliche contains even more gravel and rock fragments, sometimes rounded pebbles. The slope, the smoothness and impermeability of the hardpan, the presence of rock fragments, and the loamy nature of the soil itself, all tend to make this a very well-drained soil. It, like the hill soil, is not influenced by subterranean influx of water. Unsifted soil from near the surface possesses a water-holding power of only about 20 per cent. This low retaining power is not here due to general coarseness of the soil, but to the large proportion of angular gravel, which of course holds practically no water.

3. The soils of the wash, a broad streamway from the Tucson mountains, which cuts through the general valley floor (*Larrea* slope in this vicinity) near the northern base of the hill, vary from gravel through sand to very loamy sand. The coarser soils are practically without vegetation and are of little interest in this

connection. The loamy sand, constituting little floodplains on the margins of the actual streamway, is 30 cm. or more in depth and is underlaid by coarser material. This is the soil here considered. It is practically without gravel admixture and has a water-holding power of about 25 per cent of its dry weight. It is almost certain (but without direct evidence) that an underground water table is present here, at least for many months of the year. The soil surface is nearly level and water is received from the superficial run-off of the hill and *Larrea* slope; however, it is well drained below.

4. The soil mass of the river floodplain, now completely abandoned by the stream, is of unknown depth. The surface layer is level and composed of clay loam with a water-holding power of about 39 per cent of its dry weight. This is about 8–9 meters deep and rests on sands and gravels, permanent water being met with at a depth of 10–15 meters. This soil is characterized by general absence of surface run-off and by but slow percolation to lower layers. The dry soil of the deeper layers, however, removes moisture from near the surface as rapidly as it can move downward by capillary action.

THE PLANT SOCIETIES.—The plant societies of the area about the Desert Laboratory have been thoroughly described by SPALDING in the work already mentioned, and also in a journal article (2). THORNBER's ecologically classified list of species for this region (pp. 103–112 of the same monograph) is of especially great value to the student of environmental factors. The four types of vegetation which occupy respectively the four soil types here considered may be briefly characterized as follows:

1. The *Parkinsonia* society of Tumamoc Hill possesses more forms, both woody and non-woody, than any other of the four societies here considered. Besides this form of palo verde (*Parkinsonia microphylla*), the group includes the giant cactus (*Cereus giganteus*), the ocotillo (*Fouquieria splendens*), the barrel cactus (*Echinocactus Wislizeni*), several opuntias of both cylindrical and flat-stemmed types, *Acacia constricta*, *Larrea tridentata*, *Celtis pallida*, small specimens of mesquite, etc. *Bigelovia Hartwegii* occurs here but does not attain as great numbers or as large size as on the

river plain, where it is more characteristic. Numerous low forms are active throughout the year, notably *Encelia farinosa*, *Sphaeralcea pedata*, etc., and a great array of summer and winter forms are to be found at the proper season.

2. The *Larrea* society of the gravelly slope exhibits, in many localities, almost no woody species other than the creosote bush (*Larrea tridentata*). The bushes are uniformly and openly distributed over a surface which is otherwise nearly bare of vegetation, excepting during early spring and late summer, when numerous low forms appear. Of the desert shrubs within its climatic range, *Larrea* seems best fitted to withstand prolonged drought both of air and soil. *Ephedra* occurs upon the slope as well as in the wash, but makes its best growth in the latter place.

3. The *Cercidium torreanum* society of the wash is characterized by this form of palo verde and by mesquite (*Prosopis*), *Condalia lycioides*, and *Acacia Greggii*. The three latter forms are also characteristic of the *Prosopis* society of the plain. *Ephedra trifurca* and the creosote bush (*Larrea tridentata*) attain here their most luxuriant growth, though the latter, at least, is most characteristic of the *Larrea* society. Aside from these and some other woody plants, the vegetation of the wash consists mainly of small forms, which are active only during the periods of moist soil, either in winter or summer or at both seasons.

4. The *Prosopis* society of the river plain is dominated by mesquite, two forms of *Acacia* (*A. constricta* and *A. Greggii*), and *Condalia lycioides*. Annuals of many forms are numerous during the moist periods. The most striking of the low perennials is *Bigelovia Hartwegii*, which scarcely occurs outside this group, except for scattered plants in the *Parkinsonia* society.

METHODS OF DETERMINING AND OF REPRESENTING SOIL CONDITIONS.—The method used in determining the water-holding powers given above was to place the soil in a sheet-metal cylinder about 12 cm. high and 10 cm. in diameter, with perforated bottom (the latter covered externally with thin cloth), then to saturate the soil by standing in a vessel of water, at the same time pouring water on the soil surface, and finally to allow the soil mass to drain till no more liquid water came away below. From the weight of the

dry and saturated soil the water-retaining power is calculated in the usual way (**3**).

The actual soil moisture content was determined by the weighing and drying method, the temperature of drying being 105–110° C. The samples were taken, by digging, at depths of 15 and 30 cm. for all soils but that of the *Larrea* slope. For the latter soil, on account of its shallowness, the depths were 10 and 20 cm. Samples for each soil type were taken from the same area of a few square meters, the small excavations being immediately refilled. No later sample was taken from within 50 cm. of the soil thus disturbed. On December 13 irrigation water made it necessary slightly to change the position of the station for the soil of the floodplain, otherwise the stations remained the same throughout the whole period. Samples were taken at intervals of about 10 days. Three samplings were omitted for all soils during the month of June 1908. A few other omissions of single samples occur.

The specific gravities of these fours soils are approximately the same, there being almost no content of organic matter. Therefore the moisture contents are calculated on the basis of the dry weight of the soil and are here approximately comparable.

The careful work of Mr. J. C. BLUMER, Mr. E. E. SHERFF, and Professor J. E. KIRKWOOD, who performed the operations of collecting, weighing, and drying the soil samples, as well as that of keeping the rain record, is here gratefully acknowledged.

The accompanying graphs (figs. 1–4) have been constructed for each soil separately; the lesser depth is represented by a thin line and the greater by a heavy line. The precipitation record was kept for the hill station alone, but there is no reason to doubt that the rain record for the other stations would have been essentially the same had it been actually taken. For easy comparison, the rainfall is represented below the graphs of soil moisture simply by vertical, shaded blocks, the length of each block denoting the relative amount of precipitation which took place during the corresponding ten-day period. The figures directly above these blocks denote the precipitation in centimeters, that is, the relative length of the blocks. The data from which the moisture graphs are constructed are placed upon the figures directly above the base

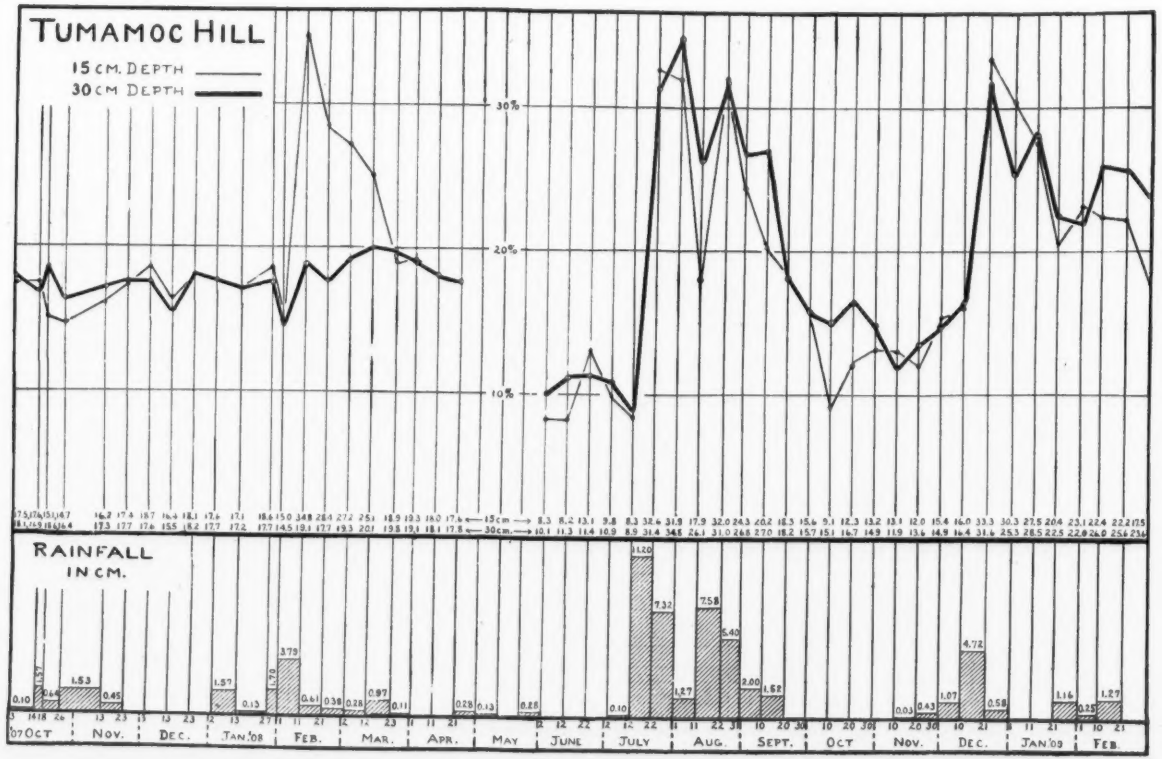
TUMAMOC HILL
15 CM. DEPTH
30 CM DEPTH
30%
20%
10%
RAINFALL
IN CM.
0.10
0.65
1.53
0.45
1.57
0.13
1.79
3.79
0.61
0.38
0.28
0.97
0.11
0.28
0.13
0.28
0.10
11.20
7.32
1.27
7.58
5.40
2.00
1.62
0.03
0.43
1.07
4.72
0.58
1.16
0.25
1.27
07 OCT
NOV.
DEC.
JAN.'08
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT
NOV.
DEC.
JAN.'09
FEB.

FIG. 1

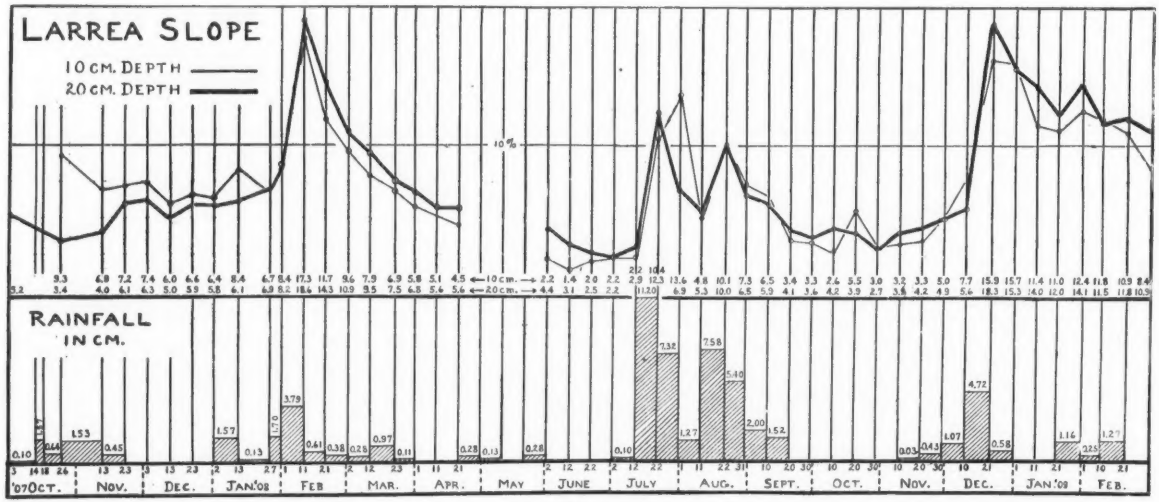
LARREA SLOPE
10 CM. DEPTH
20 CM. DEPTH
10%
RAINFALL
IN CM.
'07 OCT.
NOV.
DEC.
JAN '08
FEB
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN '09
FEB

FIG. 2

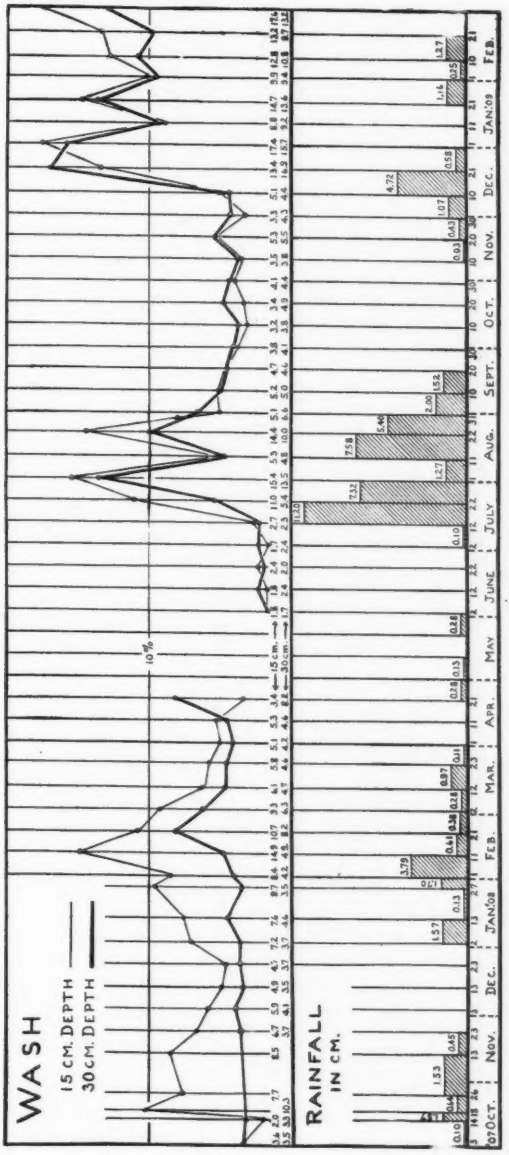
WASH
15 CM. DEPTH
30 CM. DEPTH
10%
RAINFALL
IN CM.
OCT.
NOV.
DEC.
JAN'09
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN'09
FEB.

FIG. 3

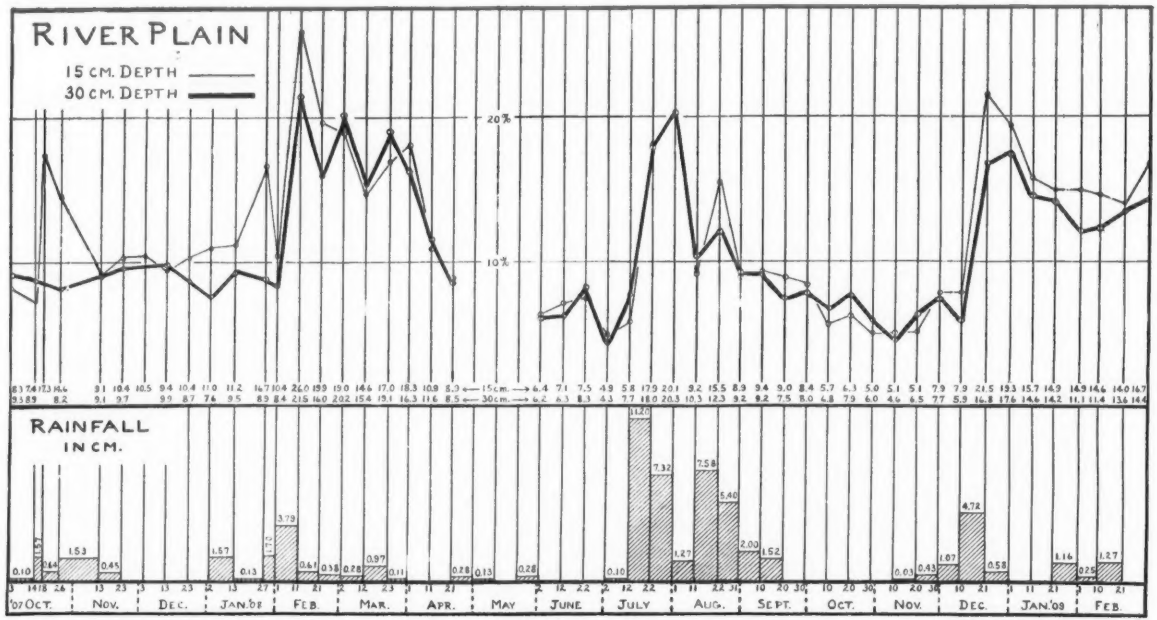
RIVER PLAIN
15 CM. DEPTH
30 CM. DEPTH
20%
10%
RAINFALL
IN CM.
'07 OCT.
NOV.
DEC.
JAN.'08
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.'09
FEB.

FIG. 4

line of these graphs. They express percentage of dry weight. At the base of each figure, the dates of sampling are indicated. The major portion of the calculations and of the drawing of the graphs are the work of GRACE J. LIVINGSTON.

DISCUSSION OF GRAPHS.—It is to be remembered that several simultaneous samples at the same station would be expected to vary to some extent, especially in the stony soil of the hill and of the deeper layer of the slope. Therefore it is not surprising to note minor fluctuations in the graphs, which do not appear traceable to conditions of precipitation.

The graphs bring out clearly the lagging of soil moisture behind precipitation; it requires considerable time for rain water to reach the upper level of sampling and a still longer time for it to reach the lower level. A slight precipitation may not alter the condition of the soil at either level, the water being lost by evaporation before it can penetrate even to a depth of 10 or 15 cm. It also occurs that a rain which is only sufficient to moisten the surface layers, thus placing them in capillary connection with the deeper ones which are already moist, may actually accelerate the drying out of the deeper layers. Thus a slight rain is sometimes directly deleterious to the vegetation; it removes the dry mulch from the surface and fails to add markedly, if at all, to the deeper moisture content, so that before the dry mulch can regenerate, the deeper soil has lost considerable water by upward movement and evaporation.

From data given in *Publication 50* of the Carnegie Institution (pp. 66, 67) it appears that a number of plants of the hill, when grown in pots (in hill soil), wilted with a soil moisture content of 6–12 per cent by wet volume. On the basis of dry weight these numbers become about 7 per cent and 14 per cent. *Boerhavia* (one of the summer annuals of the hill) wilted in the open soil with a moisture content of 6–7 per cent by wet volume, or about 7–8 per cent on the basis of dry weight. These observations were taken in July and August, the period of the summer rains, when the evaporating power of the air was far below its magnitude of May and June or of October and November. With greater evaporation rate, the plants should of course wilt with a correspondingly higher soil moisture content. It is probably safe to assume, there-

fore, that during the driest months of the year the majority of the plants of the hill require an amount of soil moisture of 8–10 per cent. With a drier soil than this it is probable that most forms without pronounced storage organs would succumb in a few weeks.

No determination of wilting points is as yet available for the other three soils, but from the well-known fact that the "non-available water" in soils decreases, in general, with their water-holding power, it is probably safe to assume that vegetation can withstand a considerably drier soil in the case of the slope and wash, and a somewhat drier one in the case of the river plain.

From the graphs it is evident that the period of most intense drought occurs just before the beginning of the summer rains. In general, the month of June may be taken as the month of driest soils, and it is also the month of greatest evaporation. Therefore, for plants without well-developed water storage tissues, this month must approximate the critical period of the year so far as the water relation is concerned. It will therefore be instructive to derive the average soil moisture content for this month in the case of each of the four soil types. So far as I am aware, the root systems of all plants of this area, which are without storage tissues and which are not annuals, penetrate into the soil at least to the greater of the two depths here considered. We may therefore consider the greater depth alone. The following table presents these averages for the four determinations taken from June 2 to July 2, 1908. The water-holding capacities are also given, and the water content as percentage of the latter.

SOIL MOISTURE AT THE CRITICAL PERIOD

| Soil type | Water-holding power, in percentage of dry weight | Average moisture content, June 1908 | | |
|---|---|---|---|---|
| | | Depth in cm. | Percentage of dry weight | Percentage of water-holding power |
| Hill | 48 | 30 | 10.9 | 22.7 |
| Slope | 20 | 20 | 3.1 | 15.5 |
| Wash | 25 | 30 | 2.1 | 8.4 |
| Plain | 39 | 30 | 6.3 | 16.1 |

That the vegetation of the hill is the most varied and the most perennially active of all the plant societies of our area, agrees well

with the high soil moisture content (almost 11 per cent) and the high percentage of the moisture-retaining power (almost 23 per cent) which this soil exhibits during the driest month of the year. It is to be remembered in this connection that the soil of the hill is often considerably over 30 cm. in depth, and that, in the dry season, the highest moisture content is to be expected just above the underlying rock surface. In the summer of 1904, immediately preceding the advent of the July rains, a soil sample from a depth of 35 cm. on the hill exhibited a moisture content of 17.9 per cent of its dry weight. From the graph of the hill soil and from this last consideration may be derived convincing additional evidence in favor of the conclusion expressed by SPALDING and by the author (*Publication 50*, Carnegie Inst., p. 12) "that sufficient moisture is probably at all times present in the deeper layers of these soils [of the hill] for the needs of transpiration and even growth." The excellent soil conditions exhibited by Tumamoc Hill are emphasized by the fact that at no time during the period of record did the observed moisture content at a depth of 30 cm. fall below 8.9 per cent, and that it was far above 11 per cent at all times excepting in the months of June and November 1908.

The soil of the *Larrea* slope, at a depth of 20 cm., just above the caliche hardpan, exhibited only 3.1 per cent of moisture as the June average. Had the soil been sifted, the moisture content would undoubtedly have been markedly greater, as is indicated by the high percentage of its retaining power (15.5 per cent) which the moisture content represents. But the amount of water available for plants must be considered as a vanishing quantity at this time.

In this vicinity, practically the only perennially active plant on the slope, excepting a few scattered cacti and here and there a plant of *Fouquieria* (itself hardly perennially active), is the creosote bush, from which the slope is named. This plant, as has been mentioned, is probably the most resistant to drought conditions of all non-storage forms in the region. An inspection of the graph for this soil brings out the fact that the moisture content rose above 10 per cent only in February and March, in July and August 1908, and in the winter of 1909. In distinct opposition to the soil

of the hill, this soil is undoubtedly deficient in moisture for by far the greater part of the year. It usually supports spring and summer annuals for a few weeks during each of its moist periods.

The soil of the wash shows an even more inadequate moisture supply for the month of June than does that of the slope. This soil contains practically no gravel in its superficial layers and its moisture content at this time (2.1 per cent by dry weight) was only 8.4 per cent of its water-holding power. From the general aspect of the vegetation it would be concluded that this soil was better supplied with moisture than that of the slope, but the graph fails to explain this view. The discrepancy is apparently due mainly to the great depth of the soil, which acts as a much more extensive reservoir for water than the shallow soils of hill and slope. The presence of underground water is doubtless effective in case of those trees and shrubs the roots of which penetrate deeply. The continuously active forms which occur here must be considered as much more deeply rooted than is possible on the hill and on the slope.

The soil of the river plain exhibits a much more favorable moisture condition, not only in June, but throughout the year, than any other of our four soil types excepting that of the hill. Its average water content for the drought period was 6.3 per cent by dry weight. In terms of its moisture-holding power, this becomes 16.1 per cent. This is a deep soil, with unknown, but surely considerable, amounts of moisture below the limits of sampling. It also has constant subterranean water at depths which can probably be reached by tree roots. This latter fact seems to explain the occurrence here of mesquite, acacia, and other deep-rooting shrubs. In the dry seasons (early summer and late autumn) this soil shows very few active plants besides those just mentioned, but in the rainy seasons it supports a dense growth of annuals, being apparently as well suited to such forms as is the soil of the hill itself. That many annuals of the hill fail generally to appear on the plain, and conversely, is perhaps to be explained by the considerably higher moisture content occurring during the rainy seasons on the former soil. It may also be related to conditions which hinder surface

evaporation on the hill, such as the presence of numerous rock fragments on or in the soil.

An interesting question is suggested by the fact that the creosote bush dominates the slope and occurs on the hill, but is almost entirely absent from the plain, excepting along the margin where it abuts against the slope. No evidence as to why this shrub should not thrive on the plain is as yet at hand. The most vigorous specimens of the area occur along the lower margins of the slope, which agrees with a similar behavior always observed in irrigated specimens, in seeming to indicate that a more adequate water supply produces an abnormally great growth. SPALDING mentions the physiographical relation (which of course cannot *directly* affect the vegetation) that *Larrea* usually dominates gentle slopes which are being eroded at the present time. It would seem that there must be some condition in the soil of the plain which is antagonistic to the growth of this shrub. A study of the oxygen conditions of these soils may possibly throw some light on the subject. The moisture condition alone is inadequate to explain the facts.

The results obtained from a study of the graphs would place the hill soil first, as the best suited for general plant activities; the soil of the plain would occupy second place, and the two other soils would lie rather close together and far below either of these. This general arrangement agrees well with the vegetational characters of the four soil types if we consider that the deep-rooting forms of wash and plain obtain moisture from levels deeper than those here considered. It is also in fair agreement with the simple series of the water-retaining powers of the four soils. From this retaining power alone the soils would have been interpreted in the same general way. This emphasizes the water-holding power as an easily obtained and very important factor in studies of distribution.

The last-named factor has been used by the writer (4) with some success in a search for the determining conditions of forest distribution in Michigan. It appears that for different upland habitats of the same region, where the level of underground water is far from the surface, and the precipitation and evaporating power

of the air are approximately uniform, the relative soil moisture conditions may be fairly well approximated by the criterion of water-holding power. The ease of obtaining comparative data for this factor entitles it to a thorough test as a soil criterion for habitat studies.

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# THE EFFECT OF LONGITUDINAL COMPRESSION UPON THE PRODUCTION OF MECHANICAL TISSUE IN STEMS

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(WITH TWO FIGURES)

## Introduction

For more than a century observations and experiments have been made to determine what factors cause or influence the production of mechanical tissue in plants. Previous to PFEFFER's time, the causes were supposed to be of a mechanical nature. These explanations have been shown to be inadequate.[1] PFEFFER (**26, 27**) showed that tension, pressure, or even contact may act as a stimulus to cause the production of more mechanical tissue. NEWCOMBE (**21**) suggested that plants must respond to stress in a self-regulatory manner by producing mechanical tissue where it is most needed. He also indicated the complex notion in regard to stress, and suggested that it should be subdivided. At present we use the terms tension or traction, and pressure or compression, to indicate two opposite kinds of stress

To determine the effect of each kind of stress, much careful experimentation is necessary. HEGLER (**12**), BALL (**1**), HIBBARD (**14**), and BORDNER (**2**) have investigated the influence of tension upon growing cells, with regard to its mechanical as well as to its stimulatory effects. Although these investigators did not agree in all points, their results show that tension alone cannot cause a very marked increase in mechanical strength. VÖCHTING (**34**), HIBBARD (**14**), and BÜCHER (**4**) have contributed a little concerning the effects of longitudinal compression.

VÖCHTING reported that he fastened weights upon the tops of sunflower stems, some of which had been decapitated, and upon Savoy cabbages, all of which had been decapitated. After leaving the plants thus weighted for several months, he was able to discover

[1] For historical account see URSPRUNG, Biol. Centralbl. 1906.

no increase of mechanical tissue in the sunflower stems, and but a slight increase in the cabbage stems, an increase not at all proportional to the weights used.

HIBBARD suspended weights upon the stems of the sunflower, periwinkle, fuchsia, and coleus, and found in all except coleus a slight response to compression by self-regulatory increase in mechanical tissue. He did not believe, however, that the evidence could be regarded as conclusive.

BÜCHER inclosed both the upper and the lower portions of stems of the castor oil plant in plaster casts, and then fastened these casts so that the stems as they elongated were subjected to a longitudinal compression. All but two of his plants became bent; the two which remained straight were weaker in mechanical tissue than normal plants.

From the few data which have been recorded, it is very plain that we do not have sufficient evidence to show whether or not compression or increased weight may act as a stimulus to cause the production of a greater amount of mechanical tissue in plant stems. General conclusions have been drawn from mere observations of phenomena, which may be due to any one of several influences or to the combination of two or more influences. The few experimental data have led to indefinite or contradictory conclusions. This investigation was undertaken to secure exact experimental data upon the effect of weight tending to produce a longitudinal compression in vertical stems.

## Materials and methods

### PLANTS USED

From the nature of the experiments, it was necessary to use plants with single upright stems. Both woody and herbaceous plants were used. The woody plants were both one-year-old shoots and seedlings of the common locust (*Robinia Pseudo-Acacia*), both young and one-year-old shoots of sumach (*Rhus glabra*), one-year-old shoots of the poplar (*Populus tremuloides*), and the castor oil plant (*Ricinus communis*). The herbaceous plants were the sunflower (*Helianthus annuus*), the broad or Windsor bean (*Vicia Faba*), and the common bean (*Phaseolus*

*vulgaris*). The experiments upon woody plants were conducted in the garden during the spring and summer; those upon herbaceous plants were conducted in the greenhouse during the winter and in the garden during the summer.

## METHODS OF EXPERIMENTATION

After many preliminary trials, the methods given below were found to be most suitable. For methods other than these, descriptions are given in the account of the different experiments in which they were used. In general, a large series of plants of the same size and age and growing under the same external conditions was used for each experiment. The plants were numbered consecutively. The height and two diameters of each plant were measured, one diameter of the part to be under compression and the other of the part above the compressed region. In case a stem was not cylindrical, the average of the greatest and the least diameter was taken as the diameter of the stem at that place. Strong cords were then looped about each stem at a suitable distance above the ground to serve as an attachment for the weights. The stems were protected from mechanical injury by the cords by first wrapping pieces of soft cloth, commonly known as table matting, around each stem. Each stem was then firmly fastened in a vertical position by tying it to stakes, not in contact with the plant, so that it could not bend or sway, and yet could be restrained in no way except by the downward pull of the weights. Weights were then suspended upon half of the plants, while the other half were left to serve as controls. All plants in a series thus treated were under exactly the same conditions, except that the lower part of each experimental plant was subjected to a compression caused by the downward pull of the weights. If the plants were practically equal in size, alternate stems were weighted; but if they happened to be somewhat unequal, care was taken to see that the average size of the experimental plants was equal to the average size of the control plants. For every large experimental plant, an equally large control plant was chosen, and for every small experimental plant, an equally small control plant was chosen.

More weights were added from time to time according to the

condition of the several experiments. In some experiments the weights were light, scarcely exceeding the weight of the plants; in other experiments they were equal to many times the weight of the plants themselves. Great care was taken to see that the stems were not bent by the weights.

## MECHANICAL TESTS

At the conclusion of each experiment, all the plants were measured in the same manner as at the beginning, and the stems taken

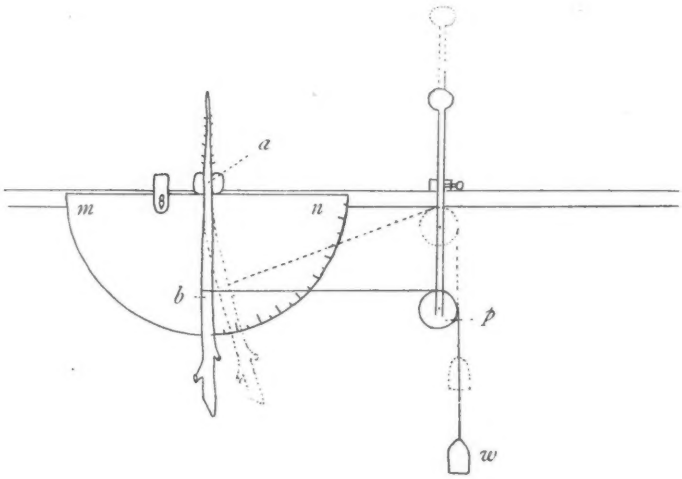


FIG. 1

to the laboratory for mechanical tests and anatomical study. The compressed part of each experimental plant, as well as the corresponding part of each control plant, was tested for rigidity, as shown by its resistance to bending, and for resistance to crushing.

The resistance to bending was determined by a simple piece of apparatus, which is represented by the diagram (fig. 1). The basal end of the stem to be tested was clamped securely at *a;* the cord was looped over the stem at *b*, always at a fixed distance from *a;* the weight *w* was then slowly released and the amount

of bending read in degrees upon the arc of the protractor *mn*. The testing weight for each series of plants was selected so that the plants would not be broken or too strongly bent. The pulley *p* could be adjusted as indicated by dotted lines, in order that the weight should at all times act in the direction perpendicular to the stem. This method was found to show very slight differences in the rigidity of stems.

The resistance to crushing was determined by the apparatus shown in fig. 2. A piece of the stem 10–15 mm. in length was placed with one end against the fixed block *f*, and the movable block *m* brought against the opposite end. The movable block was attached to the strong spring balance *s*, which in turn was attached

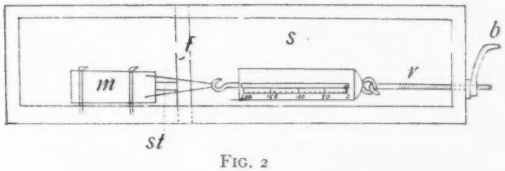


FIG. 2

to the threaded rod *r*. When the tail nut *b* was turned upon the rod *r*, the movable block *m* was drawn toward the fixed block *f*, thus subjecting the stem *st* to pressure. The amount of pressure could be read at once upon the scale of the balance. The resistance to crushing could be determined very sharply, for when the critical point was reached, the stem always gave way suddenly.

After testing a piece for resistance to crushing, the part of the stem next to that which was crushed was put into alcohol to be preserved for a study of the internal structure and microscopic measurements of the mechanical tissues.

## ANATOMICAL STUDY

The anatomical studies and measurements were made from cross-sections, which were suitably prepared and stained so as to differentiate more clearly the various tissues, principally the xylem and hard bast. Chemical reactions (aniline sulfate with sulfuric acid, and phloroglucin with hydrochloric acid) as well as stains (acid fuchsin, aniline safranin, and methyl blue) were used.

The method which gave the best results and which was generally used was as follows: Cross-sections of uniform thickness were placed in watch glasses with a little 50 per cent alcohol and two or three drops of alcoholic safranin. In the course of three or four days, all the lignified cell walls were stained a bright red, while other tissues remained nearly colorless. The sections were then either washed in water and mounted in glycerin, or washed in 96 per cent alcohol, cleared in clove oil, and mounted in balsam.

Since xylem forms by far the greatest part of the strengthening, or mechanical, tissue, more measurements were made of this than of the other tissues. For this purpose, exact camera drawings of the lignified parts were made and the area of these drawings determined by means of a polar planimeter. Thickness of wall was determined by taking the average of several measurements, which were made by means of an eyepiece micrometer. Relative size of cells was determined by counting the number in a certain field in the microscope or by micrometer measurements.

In order to avoid the danger of a personal error in making the mechanical tests and microscopic measurements, the stems were numbered indiscriminately by a second person, so that the writer did not know which were experimental and which were control plants until after all tests and measurements were made and the results copied.

## Experimental

### COMMON LOCUST (ONE-YEAR-OLD PLANTS)

In April, before the growth had begun, 14 one-year-old plants were selected from a large number of sprouts. These plants were measured, tied securely to stakes, and weights suspended upon one-half of them. The cords about the stems were shifted from time to time to avoid constricting the stems as they increased in size. More weight was placed upon the experimental plants, from time to time, as long as they continued to grow. In October, when the experiment was concluded, some of the larger stems were supporting a weight of 20 kilos.

The results for this series of plants were not satisfactory in all respects. Several of the stems were broken or otherwise injured

during the summer. The growth was very unequal in different stems. Some of them increased in size three or four times as much as others, which grew under apparently the same conditions. This is not an uncommon occurrence, however, among shoots which spring from old roots.

Careful comparisons did not show any greater increase in growth or thickness of stem in the experimental plants than in control plants. On the other hand, some of the experimental stems had smaller diameters in the compressed portion than control stems. This diameter in three stems was less than the diameter of the same stem above the compressed part. Although this difference is normally not infrequently noticed in this species, it was rather more striking than usual in these plants. Cross-sections were prepared from experimental stems, control stems, and stems which had not even been tied to stakes. No differences, however, could be seen between any of them.

### LOCUST SEEDLINGS

In order to obtain woody stems of more nearly uniform size, seedlings of locust were grown in the greenhouse and transplanted into the garden as soon as the weather became favorable in the spring. Of about 100 which were transplanted, only 30 were considered suitable for experimentation. These were prepared in the usual way and kept under experimental conditions until growth had ceased, about October 15. In the greenhouse, some of the seedlings grew to a height of 15–20 cm.; their stems, however, were very weak. When they were transplanted, they were bent nearly if not quite to the ground by every little breeze, which could scarcely bend locust sprouts which had come up in the garden. In two or three weeks' time, however, these slender seedlings, although they had grown but little in height, had become strong enough to withstand ordinary winds. Some of these slender seedlings were tied to stakes to prevent their being whipped about by the wind. Two or three weeks later, when the stakes were taken away, the plants were still unable to support themselves against a light wind.

This series was kept under the best conditions for growth. The plants were watered frequently during the dry season and protected

from all injury. The final measurements show that the plants grew well. The experimental plants increased 152 per cent in height, 131 per cent in the diameter of the weighted portion, and 122.5 per cent in the diameter a short distance above the weighted part; the control plants, in the same positions and dimensions, 142 per cent, 135 per cent, and 133.7 per cent respectively. The relative amounts of xylem for the experimental and the control plants were 95.17 and 100 respectively. Careful measurements of cell walls showed no difference between the experimental and the control plants.

SUMACH (ONE-YEAR-OLD PLANTS)

From a very large number of thrifty sumach sprouts 24 one-year-old plants were selected for experimentation. In April these plants were tied to stakes, and weights were placed upon the experimental plants in the usual manner. Conditions were fairly good during the growing season. The plants were kept under experimental conditions until October, although nearly all of the growth in size and thickness of stem took place in the spring and early summer. The final measurements and tests showed that the experimental and the control plants were practically equal in size and strength at the end of the season. A comparison of the actual increase in xylem, as determined from the annual rings, showed about 18 per cent less for the experimental than for the control plants. Careful examinations and measurements showed no difference in the size of cells or in the thickness of cell walls.

SUMACH (YOUNG PLANTS)

Sixteen young plants were placed under experimental conditions as soon as they had attained a height of about 35 cm. These plants did not increase greatly in size and thickness of stem. The tests and measurements showed that the strength and amount of xylem were very nearly equal for the experimental and the control plants. The percentage increase was somewhat greater for the experimental plants than for the controls. This difference, however, loses its significance when we observe that the actual increase in height was only 6.93 cm. for the experimental and 5.11 cm. for the control plants, and the increase in diameter only 2.07 mm. and 1.75 mm.

respectively. Careful microscopic examinations and measurements failed to show any differences in cells or cell walls.

### POPLAR (ONE-YEAR-OLD PLANTS)

Sixteen plants of the poplar were selected and placed under experimental conditions in April. The plants were measured and carefully tied to stakes. Weights were suspended upon eight of the plants, and as the plants increased in size more weights were added. Although growth practically ceased in early summer, the plants were kept under experimental conditions until October.

The final measurements and tests showed no greater increase in the experimental plants than in the control plants; the increase, in fact, was somewhat less for the former than for the latter. For the experimental plants, the increase in height and diameter of the stem was less than 16 per cent, and for the controls 20 per cent; the relative increase in xylem 77 and 100 respectively; the resistance to bending 81 and 100 respectively. It is difficult to account for these differences. Although the conditions for growth were not good, owing to partial defoliation by insects, they were the same for both experimental and control plants.

### CASTOR OIL PLANT (GREENHOUSE PLANTS)

Twenty-four plants of the castor oil plant were selected from a large number which were grown in the greenhouse. Before tying the plants to the stakes, the stems were carefully protected with pieces of table matting. Internodes of bamboo, about 10 cm. in length, were split in two and the halves bound upon opposite sides of each stem, the lower ends extending to within 5 cm. of the ground. Weights were suspended from the upper ends of these pieces of bamboo. In this way room was made for the weights to swing free from the ground, and the longitudinal pressure was confined to the lower 5 cm. of the stems. The plants were kept under experimental conditions for four weeks. The stems were 6 mm. in diameter and 15 cm. high at the beginning of the experiment; they increased about 50 per cent in diameter and 70 per cent in height during the experimental period. At the conclusion of the experiment, the experimental stems were under a pressure of about 1000 grams, equivalent to about 1.33 atmospheres.

The results of the final measurements and tests are shown by percentages. Assuming in reference to each measurement and test that 100 represents the value for the control plants, we have for the experimental plants the following numbers: height at the beginning of the experiment 97.67, at the conclusion 92.33; diameter at the beginning 100.2, at the conclusion 104.5; resistance to bending 120.6; resistance to crushing 104.2. The slightly greater bending and crushing resistances were probably due to the somewhat greater diameter of the experimental plants.

Cross-sections of the stems in this series were prepared and studied with special reference to the hard bast fibers and the collenchyma. The number of hard bast fibers in each stem was ascertained by counting. The average number for the experimental plants was practically equal to the average for the control plants. In each stem the thickness of three collenchyma walls was measured by means of an eyepiece micrometer, and from these measurements the average width of the collenchyma walls determined; there was found to be a difference of only 0.07 $\mu$ between the two averages; moreover, this excess was on the side of the control plants.

### CASTOR OIL PLANT (GARDEN PLANTS)

Eighteen castor oil plants were selected from a large number grown in the garden. These plants were tied to stakes and weighted in the usual manner. They were about 17 cm. in height and 9.5 mm. in diameter at the beginning of the experiment; they increased about 75 per cent in height and 40 per cent in diameter during the experimental period of ten days. At the conclusion of the experiment, the experimental plants were supporting 5–7 kilos each. The usual measurement and test showed no marked differences. Letting 100 represent the value for each control plant average, the following numbers represent the relative values for experimental plant average: height at the beginning of the experiment 101.3, at the conclusion 97.2; diameter at the beginning 101.6, at the conclusion 101.4; resistance to bending 101.8, to crushing 107.5; amount of xylem 109.3.

Another experiment was conducted with 30 selected castor oil

plants, which were divided into three equal sets: experiment plants, control plants, and counterbalanced plants. Each stem of counterbalanced plants was not only tied to prevent bending, but relieved from supporting the weight of the plant itself by tying a cord about the stem, passing it up over a pulley, and attaching a weight to the free end; this weight was kept practically equal to the weight of the plant. These plants were about 20 cm. in height and 9 mm. in diameter at the beginning of the experiment; during the experimental period they increased about 40 per cent in height and 22 per cent in diameter. The growth was less in this experiment than in the former experiment because of more unfavorable weather conditions. The final measurements and tests showed no more marked differences than in other experiments.

### SUNFLOWER (GREENHOUSE PLANTS)

From plants of the sunflower which were grown in pots in the greenhouse, 30 of those with straight stems of nearly uniform diameter were selected for experimentation. The stems for this experiment also were bound upon opposite sides with pieces of bamboo to localize the longitudinal compression in the lower portions. More weights were suspended upon the pieces of bamboo from time to time, until at the end of the experimental period of four weeks the experimental plants were supporting a weight of 230 grams each.

The stems were 3.5 mm. in diameter at the beginning and about 5.25 mm. at the conclusion of the experiment. Assuming that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values for corresponding measurements and tests in the experimental plants: height at the beginning of the experiment 99.8, at the conclusion 97.4; diameter at the beginning 95.9, at the conclusion 98.4; resistance to bending 66.7, to crushing 93.5. These numbers show very clearly that there was no greater increase in the experimental than in the control plants. The test for resistance to bending especially showed less strength in the experimental than in the control plants.

Although the mechanical tests would seem to show conclusively

that no increase in mechanical tissue had been caused by weight or compression, cross-sections were prepared and careful examination made to determine the relative amounts of collenchyma, hard bast, and xylem. In none of these tissues could any difference be detected between the experimental and the control plants.

### SUNFLOWER (GARDEN PLANTS)

Thirty sunflower plants were selected from a large number of plants and placed under experimental conditions in June. Longitudinal compression was confined to the lower part of the stems by using pieces of bamboo, as in former experiments. Conditions for growth were very favorable. The plants were about 15 cm. in height and 6 mm. in diameter at the beginning of the experiment; during the experimental period of nine days, they increased 100 per cent in height and 70 per cent in diameter. The weights, which were necessarily light at first, were increased daily until the average weight for each experimental plant was 1400 grams (about three atmospheres).

At the conclusion of the experiment the usual measurements and tests, with one exception, were made. Instead of determining the resistance to crushing in this series, the tensile breaking-strength was determined by means of BORDNER'S (**2**) apparatus. If we assume that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values of corresponding measurements and tests for the experimental plants: height at the beginning of the experiment 105.5, at the conclusion 110.2; diameter at the beginning 94.1, at the conclusion 99.4; resistance to bending 80; tensile breaking-strength 64.2; amount of xylem 80.4. These numbers show that, although the amount of growth in both the experimental and control plants was practically equal, the gain in strength and in mechanical tissue was less in the former than in the latter. The heavy weights evidently retarded the production of mechanical tissue.

A second series of 24 somewhat older sunflower plants was placed under experimental conditions in the usual manner by tying the

plants to stakes and suspending weights upon half of the stems. The plants were 22 cm. in height and 8 mm. in diameter at the beginning of the experiment; they increased about 140 per cent in height and 50 per cent in diameter during the experimental period. The final measurements and tests showed very little difference between the experimental and the control plants.

A third series of 81 selected sunflower plants was divided into three sets and placed under experimental conditions. The first set consisted of 29 experimental plants, the second set of 29 control plants, and the third set of 23 control plants which were relieved from supporting their own weight by cords looped around the stems, passed over pulleys above the plants, and attached to weights, which were kept sufficiently heavy to counterbalance the weight of the stems. The plants in this series were about 38 cm. in height and 10 mm. in diameter, and were kept under experimental conditions ten days. During that time they increased 80 per cent in height and 35 per cent in diameter. Weights were added daily until each experimental plant supported 6–7 kilos.

The usual measurements and tests showed a very great similarity in every respect in all three sets. In no case was there a difference of more than 6.1 per cent between the averages for any two sets. The relative resistance to bending was as follows: experimental plants 106.1, control plants 100, counterbalanced controls 96.2. The relative amount of xylem was: experimental plants 103; control plants 100; counterbalanced controls 98.

### WINDSOR BEAN (GREENHOUSE PLANTS)

Several experiments were conducted in the greenhouse with the Windsor bean. Experimental plants tied to stakes and with the longitudinal compression localized in the lower portion, control plants tied to stakes, counterbalanced controls, and plants which grew normally, without additional weight or support, were compared with reference to strength of stem and amount of mechanical tissue. In no case did additional weight or decreased weight seem to have any influence upon the plants. Stems of plants which had been tied to stakes were found to be slightly weaker than stems which had not been tied.

COMMON BEAN (GARDEN PLANTS)

Twenty-four plants of the common bean were selected and placed under experimental conditions. The longitudinal compression was localized in the lower parts of the stems by means of the pieces of bamboo. Measurements and comparisons showed no greater gain in mechanical tissue in the experimental plants than in the control plants.

## Discussion

The question of growth and increase of mechanical tissue with special reference to compression may be considered under five heads: (1) heredity and variation; (2) correlation; (3) mechanical effects of compression; (4) stimulatory effects of compression; (5) compression in connection with other stimuli.

HEREDITY AND VARIATION

The production of a certain amount of mechanical tissue in plants is a specific characteristic just as much as is the production of leaves of certain form. Just as leaves of a given species may vary in number and size under the laws of fluctuating variability, so may the amount of mechanical tissue vary. Entirely independent of any known cause, sudden variations may occur in the amount of mechanical tissue formed. The best illustration of this sudden variability is furnished by *Oenothera lata* (DE VRIES **9**), a mutant which does not produce enough mechanical tissue to support its own weight. Another common illustration is furnished by certain laciniate-leaved varieties of the sumach, which have stems too weak to bear their own weight. The difference in the amount of xylem in closely related forms is shown in many grafts. When a scion of one species of elm is grafted upon another species or variety, it soon becomes larger than the branch upon which it was grafted, although there is more mechanical strain upon the branch than upon the scion. The same phenomenon is frequently seen in grafts upon fruit trees.

All of my experiments, especially those in which the weight of the plants was counterbalanced, showed that it is characteristic of each of the species to produce a certain amount of mechanical

tissue. It may be that at some time in the history of a plant it was susceptible to mechanical stresses, and that as a result of these stresses the plant gradually came to develop normally a certain amount of mechanical tissue without regard to the stresses to which it might be subjected. Whether this is the case or not is a mere matter of speculation, so far as this work is concerned, since of course experiments can throw no light upon that phase of the problem. Yet some plants may still be able to respond in a slight degree to such stimuli. It was with this possibility in mind that such comparatively large numbers of plants were used and careful measurements made in order that individual variations might be obliterated in the average of a large number.

It is possible and even altogether probable that the importance of such differences and variations may not have been given the proper amount of attention, or that they may have been overlooked entirely. In this work, however, the possibility of an error from both specific and individual variation has been eliminated by getting the averages of a large number of the same species for each experiment. Further discussion of this phase of the question, therefore, may be omitted. Heredity, however, does have a very important bearing upon the problem in another way.

The ability to produce certain tissues may be hereditary but latent in a plant, and require a certain definite stimulus to make it appear. Many plants do not produce leaves unless they feel the stimulus of light; others, cacti for example, produce leaves only when deprived of light. The experiments of VON DERSCHAU (**35**) and WORGITZKY (**37**) show that mere contact may cause the production of a certain amount of mechanical tissue, and contact and strain together are necessary to cause a tendril to produce its normal amount of mechanical tissue. The results of my experiments show that, at least in the plants which were used in this work, no latent hereditary activity is brought forth by compression.

## CORRELATION

Under this head may be considered all those observations upon the mechanical tissue in fruit-bearing stems and branches. DENNERT (**6**), REICHE (**29**), and PIETERS (**28**) found in the great num-

ber of instances which they investigated that anatomical changes resulting in greater strength go hand in hand with the development of the fruit. These changes have been attributed both to the strain which is caused by the weight of the developing fruit, and to greater growth activity which is due to the carrying of the greater amount of building material which the fruit demands. KELLER (**16**) affirmed, however, that the fruit-bearing axis is not strengthened by strain or fruit-bearing in itself, but that the bending of the stem from the orthotropic to the plagiotropic position causes the anatomical changes. It is evident that these observations cannot throw any light upon the stimulatory effect of a tension or a compression acting alone. An experiment by VÖCHTING (**34**), however, does have a more direct bearing upon the question. He found that by removing the flower buds he could greatly retard the development of the mechanical tissue; the plants were sunflowers and fruiting stems of the Savoy cabbage. He also found that by stress brought about by weighting he could not cause the mechanical elements to reappear (the discussion of this stress is taken up in another place), but when he grafted a scion upon a decapitated stem, the cambium at once began to form the mechanical elements again, although the weight of the scion was equal to only a fraction of the weights which he had placed upon similar plants without result. He sums up the results of his experiments in the following words:

> Aus dem mitgetheilten folgt, dass der ontogenetische Gang der Gewebedifferenzierung von inneren, correlativen Verhältnissen beherrscht, dass die Bildung der einzelnen Gewebeformen nicht einfach durch das Bedürfniss bestimmt wird. Die Auslösungs-Theorie genügt hier nicht.

This experiment shows very clearly that correlation may have much more to do with mechanical tissues than mere stress or strain.

Correlation is also seen in many trees in which one-sided growth in the wood is correlated with a greater development of the root system on that side, or with the greater number of branches and the correspondingly greater leaf surface of that side. KNY (**17**) asserted that one-sided leafing of a tree must be associated with one-sided increase in the growth of the trunk. HARTIG (**10**) reported that this is the most common cause of eccentric growth in

pine trunks, although there were exceptions to the general rule. WIESNER (**36**) has attempted to explain eccentric growth in branches by attributing it to unequal size and distribution of the leaves.

In accordance with the observations given above, it was found necessary to keep in mind constantly the correlation between the growth of mechanical tissue and the growth of other parts of the plant. Locust shoots, which at one time were apparently equal and growing under equal conditions, were found to develop at very unequal rates, apparently because of differences in the amount of nutriment stored in the roots from which the separate shoots had sprung.

The differences in herbaceous stems under different conditions are perhaps best illustrated by sunflowers which were grown in the greenhouse and plants of the same kind and age which were grown in the garden. The tall, slender greenhouse plants at the end of four weeks had such poorly developed xylem cylinders that many of the stems were not able to support the weight of the tops, while the garden plants in the same time had become strong and robust, with well-developed xylem cylinders. This is, of course, an extreme case. Many plants, however, which were grown under apparently the same conditions had to be rejected because of abnormalities or differences in growth. By selecting plants which were as nearly uniform as could be obtained, and by keeping all conditions of growth as nearly equal as possible, it was thought that accurate results could be obtained, especially since the possibility of a personal error was also excluded.

## MECHANICAL EFFECTS OF COMPRESSION

The textbooks assert that pressure, or compression, retards growth and may completely stop it if the pressure is great enough (PEIRCE **24**, JOST **15**, PFEFFER **26**). It seems no more necessary to make this assertion than to assert that heat, for example, may retard growth or even kill the plant if the temperature be high enough. It is of importance, however, to know whether retardation is proportional to the pressure, and whether changes take place in the cell or in its walls.

The effect upon the plastic growing cell must be the same whether it is compressed or whether it meets resistance to further growth. There can also be no difference in the hydrostatic or the osmotic pressure within the cell, whether the pressure be in one direction or another. In stems a longitudinal pressure causes the cells to exert a greater lateral pressure upon each other, and *vice versa* a lateral pressure must cause them to exert a longitudinal pressure upon each other.

Earlier writers assumed that growth must be inversely proportional to the external pressure exerted upon the growing cells. According to this view, the greatest growth must be in the region of the least pressure. It was upon this assumption that DETLEFSEN (**7**), SACHS (**30**), NORDLINGER (**23**), and KNY (**17**) sought to explain the eccentric growth of stems and branches. They had then merely to account for a loosening of the bark in some way to cause increased growth. DE VRIES (**8**) would account for the annual rings by assuming that the bark pressure is greater at some seasons of the year than at other seasons. The experiments, in which he retarded growth and caused the production of smaller cells by putting ligaments around the trunk, showed that great pressure may retard growth, but his relieving pressure by cutting the bark with a knife produced traumatic effects and not true growth. KRABBE'S (**18**) experiments proved that these theories for unequal growth were erroneous, for he showed that the bark pressure is never great enough to retard growth. This was an indication that growth cannot be directly or indirectly proportional to the pressure. This point was still further emphasized and cleared up by PFEFFER (**25**). PFEFFER says also (*Plant Physiology* **2**:125):

> When a root pushes an object in front of it, its rapidity of growth is not perceptibly affected unless the resistance offered is very great.

Although the living protoplasm must control in a large measure the manner in which the cell meets external compression, this subject is discussed under the head of mechanical effects rather than in connection with compression as a stimulus. The manner in which the cell meets external resistance is best told by PFEFFER (*op. cit.*, p. 124):

> Under such circumstances [when a plant part is compressed] the tension of the cell walls is gradually replaced by the external pressure, against which the whole osmotic pressure finally acts.

It is thus seen that the plant does not meet a compressing force by growth and cell division, but by osmotic pressure. In reference to growth activity in cells under compression, NOLL's (**22**) experiment seems very significant. He showed that in bent roots secondary roots do not arise from the concave side where the cells must be compressed.

HARTIG (**11**), CIESLAR (**5**), and SONNTAG (**31**) attributed the increased thickness of cell walls in heartwood to pressure. Now it does not seem reasonable to think that pressure could cause the walls to become thicker, unless it acts as a stimulus merely to cause greater protoplasmic activity. Since the plant opposes external compression, or resistance to growth, by its osmotic pressure, it would be detrimental to the plant to have the walls lignified before their limits of expansion had been reached. That secondary thickening does not take place until the extension of the cell wall has ceased seems to be the general rule. PFEFFER (*op. cit.*, p. 27) says:

> After the stretching growth of the cell has ceased, the cell wall commonly undergoes secondary thickening;

and again (*op. cit.*, p. 32):

> An intimate correlation exists between the different forms of growth, and the thickening, cuticularizing, or lignification of the cell wall usually take place when the external growth has ceased.

In regard to the part which the increase in thickness plays in overcoming resistance, we may again quote PFEFFER (*op. cit.*, p. 124):

> Even when external growth has ceased, the thickening of the cell walls may still further increase the pressure which the growing tissue is capable of exerting. The observed pressures, however, are *not* greater than could be produced by the osmotic pressure *alone*.

BÜCHER (**4**) found in his "kamptotrophic" and "geotrophic" stems that thickening of cell walls was always retarded in the parts of the stem which were under compression.

The best experimental evidence of the effect of pressure upon cell walls was given by NEWCOMBE (**20**). Plant stems were inclosed

within plaster casts; as they increased in diameter, the pressure became greater. It was found that under these conditions the cells remained alive and active, yet the walls remained thin. Even the walls which had already begun to thicken ceased to become thicker as pressure increased.

My experiments in which very young sunflower stems were subjected to heavy weights showed fairly well the retarding effect of a longitudinal compression, for the amount and the strength of the mechanical tissue was found to be less in the experimental than in the control plants.

### THE STIMULATORY EFFECTS OF COMPRESSION

Very little is to be found in botanical literature upon longitudinal pressure, or compression, as a stimulus, and still less as to its effect or lack of effect upon mechanical tissues. In nearly every instance in which the stimulatory effect of pressure is mentioned, it is loosely applied or very evidently connected with other causes of stimulation. PFEFFER states (*op. cit.*, p. 124):

> Various stimulatory influences are exercised by tension, pressure, and mechanical vibrations or disturbances.

What he says concerning the influence of compression has already been discussed under mechanical effects.

In nearly all researches, compression has been associated with other stimulatory influences. Those observations in which the author attributed the observed effects to pressure, or compression, are discussed under this head.

HARTIG (**10**) found that trees which were subjected to the action of a west wind produced thicker annual rings upon the east side than upon the west side. His explanation is best given in his own words:

> Der Druck des Windes übt einen Reiz auf das Plasma der Cambiumschicht aus, welche in zweckentsprechender Weise durch gesteigertes Wachsthum und durch Dickwandigkeit der Organe auf diesen Reiz reagirt.

These observations have not been confirmed by experiment, and URSPRUNG (**32**) has shown by his observations and experiments that longitudinal compression cannot account for these phenomena.

CIESLAR (5) bent four young spruces at right angles so that the upper parts lay in a horizontal plane, and kept them bound in that position for two years. He found the greatest increase in the thickness of annual rings to be in the concave or compressed side. From this experiment he concluded that pressure causes the greater increase in growth. The objections to this conclusion, however, are obvious. CIESLAR apparently did not consider the tension upon the convex side, nor the one-sided effect of gravity, which must produce a geotropic influence as soon as the tree is bent from the perpendicular position. The same objections may also be made to SONNTAG'S (31) conclusions.

VÖCHTING'S (34) experiments, however, require more consideration. VÖCHTING'S report of his experiments leaves room to question whether his plants were placed under longitudinal compression, tension, or a combination of the two. After finding that sunflower and cabbage plants, which had been decapitated to prevent fruiting, did not produce the normal amount of mechanical tissue, he says:

> Zunächst und vor allem fasste man die mechanischen Zellen in's Auge. Nach HEGLER'S bekannten Angaben kann man durch künstliche Belastung nicht nur eine raschere Entwickelung dieser Elemente herbeiführen, sondern ihre Neubildung sogar an Orten bewirken, an denen sie sonst nicht entstehen. Ist diese Angabe, die durch unsere eigenen Erfahrungen nach gewissern Richtung bestätigt wurde, richtig, dann darf man erwarten, dass die veränderten Objecte unseres Versuches, wenn künstlich belastet, die mechanischen Elemente wieder hervorbringen. Von dieser Voraussetzung ausgehend wurden am Blühen verhinderte Pflanzen des Wirsing und der Sonnenblume durch Gewichte belastet, die in geeigneter Weise am Scheitel angebracht waren; bei der zuletzt genannten Pflanze wurden ausserdem noch normal blühende Objecte zum Experimente verwandt. Die Belastung war verschieden gross; die grösste betrug bei der Sonnenblume 20 Kilo, beim Wirsing mehr als 6 Kilo, Gewichte, die das der Blüthen- und Fruchtstände, welche, unter gewöhnlichen Verhältnissen von der Pflanze erzeugt werden, um ein Vielfaches übertreffen. Die Belastung dauerte Monate lang.

If we understand by this that the writer had in mind HEGLER'S (13) experiments in which stems were subjected to tension or pull, we should take this "geeignete Weise" to mean that weights were fastened so as to exert a pull upon the stems. This is the interpretation placed upon it by BALL (1), HIBBARD (14), and BORDNER (2).

If, on the other hand, we take the meaning in the general sense, that a plant responds to the demands ("das Bedürfniss") made upon it, we may interpret the phrase to mean that he fastened the weights in such a way as to simulate the tension caused by the fruiting head. BÜCHER (4) interpreted this to mean a longitudinal pressure or compression, as indeed it must if the fruiting heads remained erect. Since, however, the fruiting head of a sunflower droops, it must exert tension upon the part of the stem next to it, and both tension and compression in the bent part, tension upon the upper or convex part and compression upon the under or concave part. It seems from a later statement of VÖCHTING's that the stems were kept erect. In that case, the "Belastung" must have exerted a compression only. He says in summing up his results:

> Wir fanden, dass selbst sehr starke Belastung der *aufrechten* am Blühen verhinderten Objecte nicht genügt, um das normale Holzwachsthum wieder herbeizuführen.

BÜCHER found weaker development of the mechanical tissues and less cambial activity in the two castor oil plants which he subjected to longitudinal compression than in normal plants. The stems were also larger in diameter, owing to the abnormally large thin-walled cells.

HIBBARD (14) used the same general method for subjecting stems to compression that I have employed in this investigation. His experiments were of a preliminary nature, comparatively few plants were used, and there is no record of his making mechanical tests or exact measurements of the mechanical tissue. When so few plants are used and no averages made, errors from individual variation may easily occur. It is not certain that the possibility of personal error was eliminated, although he says that the same conclusions were arrived at by two persons working independently.

In reference to HIBBARD's experiments as well as to my own, a question may arise as to whether a stimulus is really exerted by such means as were used. This question may be answered in several ways. It is well known that living protoplasm is very sensitive. This sensitiveness is shown by the responses of *Mimosa*

leaves and by tendrils. The researches of BOSE (3) have shown that the protoplasm of other plants and plant parts is equally sensitive, although the plant cannot respond by a perceptible movement. In case growth is retarded, as it was in some of the experiments, the protoplasm must necessarily feel the effect. It has been demonstrated that there are interacting stresses in plants, of which a good example is afforded by twisted tree trunks. Force is required to cause such a twisting. If the weight of the top is the force, twisting must be accompanied by a shortening of the central cylinder or by an elongation of the outer layers. In either case, a longitudinal compression must be exerted upon the outer cells. It is not certain that the inner cylinder may become shorter, but it has been shown that wood cells may increase in length from the center to the circumference of a tree trunk. If this elongation of cells tends to lengthen the outer layers of wood in straight trunks, increased weight upon the trunk must alter the internal equilibrium of stresses, for it not only acts directly upon the outer layer, but it tends to increase the retarding action of the inner cylinder. Moreover, it is not safe to say that the woody cylinder is so rigid that it cannot change, for we know that wood is more or less elastic, and that the limit of elasticity may be exceeded by either great pressure or great tension. If a bar of wood is forcibly bent and kept in that position for some time, a readjustment takes place so that the bar remains bent without the external force. The sensitive protoplasm in a cambium layer, which surrounds closely a cylinder of wood, must feel very slight changes that might occur in the cylinder.

If the weight of the plant can furnish a stimulus for production of increased mechanical tissue, this stimulus must be lacking when the stem is relieved from supporting the weight of the plant. For the same reason an increased weight, equal to two, four, ten, or twenty times the weight of the plant, ought to produce a response by an increase in the strengthening tissue. Assuming that plants do respond to various stresses by becoming stronger, and that they remain weak if relieved of all stress, then the plants used in my experiments were placed under the most favorable conditions to respond to a given stress, for they were relieved of all stress except

the downward pull of the weights. In no case, however, were they found to become stronger mechanically. It must be concluded that a longitudinal compression, acting by itself and acting continuously upon a plant stem, cannot stimulate it to greater activity, nor to an increased strengthening of the tissues that are already present.

### COMPRESSION IN RELATION TO OTHER STIMULI

For convenience, we may separate the stimulatory influences into three groups: the so-called internal stimuli, environmental stimuli, and strains or stresses. These internal stimuli may be due indirectly to environmental conditions. Since we know little or nothing about them, it is convenient to refer to this group all those phenomena which we cannot attribute to definite external conditions or stimuli. Environmental stimuli include gravity, light, heat, moisture, etc. Strains or stresses are tension and compression.

In nature the various influences are intimately associated with each other, and often so modify one another that observers and sometimes experimenters have overlooked certain influences and thus given undue weight to others. As an example we may speak of HARTIG'S observations and CIESLAR'S experiments in which pressure only was considered, where evidently gravity, tension, and perhaps other influences may have played an important part.

Others, who were not able to account for observed phenomena by certain external stimuli, explained them by saying that they are due to internal stimuli. As an illustration, a quotation from MASSART (**19**) will serve very well. In speaking of root swellings and eccentric growth in *Ficus* roots he says:

> L'épaississement asymétrique est régi par la gravitation, par la lumière et par des excitants internes, encore indeterminés.

Experimenters who examine more closely into the reactions of plants are forced more and more to the conclusion that the plant acts as a unit in a self-regulatory manner to bring about the greatest good to itself. NEWCOMBE (**21**) was the first to point out the necessity of considering the self-regulatory power of plants with special reference to their response to stress. URSPRUNG (**32, 33**) came to practically the same conclusion after a series of observations upon eccentric growth in trunks and branches.

BÜCHER (4) also arrived at this conclusion as a result of trying to bring his results into harmony with BALL'S (1) conclusions.

The application of the self-regulatory theory may seem to serve merely as a term to cover our ignorance. In reality it throws much light upon the whole question of stimulatory reactions, since it shows the great number of possibilities. In order to determine the influence of one factor, all the others must be taken into consideration, and their influence either eliminated or equalized by the use of both experimental and control plants under exact experimental conditions.

Considerable investigation has been carried on with respect to the various environmental stimuli. Further discussion of them, however, is not necessary in this place. In regard to the stimulatory effect of stresses and strains, comparatively few exact data have been obtained.

If we consider BORDNER'S results in regard to tension, it seems that a little more definite conclusion may be drawn from BÜCHER'S, as well as from my own experiments. BÜCHER found that when a stem is bent and then placed upon a klinostat the cell walls on the convex or tension side become thicker, and on the concave or compression side the walls remain thin, while the cells themselves become larger. In stems which were held in a horizontal position so that they could not bend upward under the stimulation of gravity, he observed the same results; the upper or stretched side had normal or slightly smaller cells with thickened walls, while the lower side had large thin-walled cells. Now BORDNER'S results show that, under proper experimental conditions, tension causes a strengthening of stems by producing thicker walls; and it is shown that compression, when not too great, causes large thin-walled cells. It seems reasonable to say that tension and compression may be given as the two direct influences for the results observed by BÜCHER.

It is evident that the tension and compression do not have exactly opposite effects. We have seen that compression causes the cells to become larger and thus give greater surface for the osmotic pressure. Tension, as shown by the experiments of NOLL and HEGLER, tends to accelerate growth and cell division.

The two influences of tension and compression are thus both favorable to increase in the size of the organ subjected to them. Then if we accept the view of HEGLER and BORDNER, that tension may cause the walls to thicken, we have in an alternation of tension and compression all the necessary stimuli for increased size, growth, and strength in the part subjected to those stresses. It does not seem unreasonable to assume that intermittent or alternating compression and tension should have a greater stimulatory effect than a constant stress. It is very possible that under constant stress the internal equilibrium of stresses may come in time to be readjusted so that the external stress would be no longer felt. In experimental work this objection may be removed in part by increasing the stress from time to time. Yet it is easy to see that this could not have so much influence as the complete reversing of the stress from tension to compression and *vice versa*.

## Summary

In the foregoing work the four woody stems show no increase in mechanical strength or in the amount or kind of mechanical tissue under the influence of longitudinal compression.

In young herbaceous stems the development of mechanical strength in the tissues is somewhat retarded by a longitudinal compression caused by comparatively heavy weights.

Neither light weights nor heavy weights have any appreciable effect upon the growth and strength of herbaceous stems which have already formed a cylinder of mechanical or woody tissue.

Continuous longitudinal compression causes no marked differences in the size or form of any part of the stem which is subjected to the compression, excepting of course mechanical changes which might be caused by excessive compression.

The investigation for which these results were obtained was carried out under the direction of Professor F. C. NEWCOMBE, to whom I wish to acknowledge my sincere thanks for his kindly interest and timely suggestions.

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# THE NORTH AMERICAN SPECIES OF STEREOCAULON

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(WITH NINE FIGURES)

The American species of *Stereocaulon* fall naturally into two groups. One is a typically boreal group, with *S. paschale* the central species, and a general distribution throughout British North America and the northern United States, as far south as North Carolina in the Alleghany Mountains, and in the Rocky Mountains extending into Colorado, and in the case of some of the species even into the mountains of Mexico and the South American Andes. The other group is a tropical one, represented by *S. ramulosum* and its allies, and characteristic of tropical America, from which it extends rather widely into the southern hemisphere. No American herbarium contains sufficient material for a satisfactory study of these tropical species, and for that reason the present paper is confined to a consideration of the boreal species.

Anyone who has attempted to determine material of *Stereocaulon*, or has studied the material in our herbaria, must have realized the confusion which exists in regard to the distinctive characters of the species. This confusion arises in part from the great variability of the species, and their tendency, in some cases, to intergrade. But another cause of the confusion comes from the lack of literature available to the general student and containing comparative notes on the species. This lack of comparative notes makes TUCKERMAN'S *Synopsis of the North American Lichens*, which has been the guide for most of the study of the American material, a difficult treatment to use. The classic work on the genus *Stereocaulon* is to be found in the papers of TH. M. FRIES, his *De Stereocaulis et Pilophoris commentatio* being published in 1857, and his *Monographia Stereocaulorum et Pilophororum* in 1858. These must form the basis for any careful study, but unfortunately they are rather inaccessible to American students.

The present paper is an attempt to clear up some of the existing

confusion and to provide an available account of the North American species of the boreal group, which shall include comparative notes, and shall cite the specimens to be found in some of our herbaria. I have been fortunate in having access, through the courtesy of Professor FARLOW, to the Tuckerman Herbarium, which contains authentic material of the following species:

S. coralloides Fr., S. denudatum Flke., S. nanodes Tuck., S. paschale var. conglomeratum Fr., S. tomentosum Fr., S. Wrightii Tuck., S. cereolinum Koerb., S. Despreaultii Del., S. glaucescens Tuck., and S. tenellum Tuck.

Professor FARLOW's own herbarium contains an authentic specimen of *S. foliiforme* Hue; and Professor FINK has kindly communicated a specimen of *S. alpinum* Laur. from LAURER's herbarium, which I have taken to be authentic.

In addition to the Tuckerman collection (cited as "Tuck"), the following herbaria have furnished the basis for study. The abbreviations in parentheses are those used in the body of this paper in the citation of specimens.

1. Cryptogamic Herbarium of Harvard University, including the personal collection of Professor W. G. FARLOW. (H)

2. Herbarium of Wellesley College. (W)

3. The CLARA E. CUMMINGS lichen collection, Wellesley College. (CEC)

4. The C. J. SPRAGUE collection at the Boston Society of Natural History. (BSNH)

5. Herbarium of the Thoreau Museum of Natural History, Middlesex School, Concord, Mass. (Th)

6. Herbarium of the University of Vermont, including the collections of C. C. FROST and Dr. C. G. PRINGLE. (UVM)

7. Herbarium of Brown University. (B)

8. Herbarium of Yale University. (Y)

9. Herbarium of the New York Botanical Gardens. (NY)

10. He barium of the Geological Survey of Canada. (Can)

11. The Mt. Desert Herbarium (in the possession of Mr. E. L. RAND). (Mt.D)

12. Herbarium of Professor BRUCE FINK, Oxford, Ohio. (F)

13. Herbarium of L. W. RIDDLE, Wellesley, Mass. (R)

If my interpretation of the principles of generic nomenclature

is correct, ACHARIUS should be cited as having definitely established the genus *Stereocaulon* in *Methodus Lichenum* (1803), p. 314, with *Lichen ramulosus* Swartz as the type species. It is true that the name had been used by three previous authors, but none of these can be held to have established the genus, according to present ideas. SCHREBER first published the name with a brief diagnosis in LINNAEUS' *Genera Plantarum*, ed. 8 (1791), p. 768, but no species is cited under the genus. SCHRADER, in *Spicilegium Florae Germanicae* (1794), p. 113, used the name with a single species, *S. corallinum*, a species based, however, on an imperfect lichen which later proved to be a *Pertusaria*. Finally, HOFFMAN, in *Deutschlands Flora*, II (1795), p. 128, gives a genus *Stereocaulon*, with nine species; of these nine only three are now recognized as belonging to the genus, the others included two species of *Sphaerophoron*, one *Collema*, one *Lichina*, and two imperfect forms; HOFFMAN'S genus, therefore, "embraced elements altogether incoherent" and hence cannot be considered valid. ACHARIUS thus remains the first author to place the genus on a solid foundation. The generic characters may be stated as follows:

Thallus of two parts, a primary horizontal thallus, which in most cases soon disappears, and erect, solid, cylindrical, ecorticate podetia; thallus of minute, rounded or irregularly flattened squamules, which are typically gray, sometimes creamy or white, and which also cover the podetia more or less thickly; apothecia lecideine; spores fusiform to acicular, hyaline, plurilocular. —Closely related to *Cladonia*, from which it differs in the solid podetia and the plurilocular spores, the latter character also serving to distinguish this genus from *Pilophorus*.

The term "squamules" (used by ACHARIUS, E. FRIES, SCHAERER, and others) is here adopted, in preference to the term "phyllocladia" (used by TH. FRIES and by TUCKERMAN), for the thalline outgrowths which constitute the thallus of species of the § PROSTEREOCAULON, and which occur so characteristically on the podetia of all species. The term is in current use for such thalline structures in other genera of lichens, and especially in the genus *Cladonia*, with which the squamules of *Stereocaulon* are strictly homologous, although somewhat modified.

In the descriptions of the species I have made no attempt to describe all the details of the plant, many of them unimportant,

but rather to give a diagnosis of the salient and characteristic features by which the species is to be recognized.

KEY TO THE SPECIES

This key is based on typical specimens. For the determination of intergrading forms, reference should be made to the comparative notes, which follow each species.

A. Plants chalky-powdery ..... 9. *S. albicans*
AA. Plants not chalky-powdery.
  B. Primary thallus present.
    C. Spores 4 μ wide, ends blunt; podetia frequently ending in soredia ..... 1. *S. pileatum*
    CC. Spores 2.7 μ wide, ends pointed; podetia never ending in soredia ..... 2. *S. condensatum*
  BB. Primary thallus absent.
    C. True squamules absent, podetia ending in flattened, foliose tips ..... 8. *S. Wrightii*
    CC. True squamules present.
      D. Squamules of the palmate-digitate type (see fig. 7).
        E. Podetia glabrous or faintly tomentose, cephalodia with *Stigonema*.
          F. Podetia loosely branched and spreading 4. *S. paschale*
          FF. Podetia in compact cushions 4*a*. *S. paschale* v. *conglomeratum*
        EE. Podetia more or less densely tomentose, cephalodia with *Nostoc*.
          F. Podetia repeatedly branched 5. *S. tomentosum*
          FF. Podetia subsimple 5*a*. *S. tomentosum* v. *simplex*
      DD. Squamules of some other type.
        E. Squamules coralline ..... 3. *S. coralloides*
        EE. Squamules umbilicate or coarsely granular.
          F. Podetia glabrous, cephalodia with *Stigonema* 7. *S. denudatum*
          FF. Podetia tomentose, cephalodia with *Nostoc* 6. *S. alpinum*

## Section PROSTEREOCAULON

Primary thallus persistent and closely adnate to the substratum, podetia mostly short, under 2 cm., and simple or sparingly branched;

squamules poorly developed, mostly granular.—The species of this section show resemblance to *Pilophorus*.

KOERBER'S name "Cereolus" for this section must be abandoned, with the exclusion of the *Lichen cereolus* of ACHARIUS from the genus (see discussion under *S. pileatum*).

1. STEREOCAULON PILEATUM Ach.

*S. pileatum* Ach. Lich. Univ. p. 582. 1810.

*S. condensatum* Laurer in Fries Lich. Eu. p. 203, in part. 1831; and in Tuck. Syn. Lich. New Eng. p. 46, in part. 1848.

*S. cereolus* Schaerer Enum. Crit. Lich. Eu. p. 178. 1850; not Ach. Meth. p. 316. 1803.

*S. cereolinum* Koerber Syst. Lich. Germ. (1855) p. 14. 1855; not Ach. Syn. p. 285. 1814.

Primary thallus persistent, closely adnate to the substratum, formed of granular squamules which tend to become coralline; podetia short, mostly under 1 cm., and simple or nearly so, glabrous, with scattered coralline-granular squamules; apothecia terminal, or often absent and the podetia then ending in a mass of white soredia; spores 16.5–29×3.5–5 $\mu$, average 21.4×3.9 $\mu$, with blunt ends; cephalodia of the type of *S. paschale* (*q.v.*).—Growing on rocks.

SPECIMENS EXAMINED

EUROPE: Stenh. Lich. Suec. no. 85; Moug. and Nestl. no. 947; Koerb. Lich. sel. Germ. no. 271.

CANADA: Newfoundland, *Waghorne* 1893, as *S. nanodes* (Hb. Eckfeldt); Anticosti Is., *Macoun* Aug. 24, 1883 (Can); Cape Breton Is., *Macoun* July 22, 1898 (Can); Nova Scotia, *Macoun* 1883 (Tuck); *McKay* (BSNH); Grand Manan Is., *Willey* (BSNH).

MAINE: Mt. Desert, *J. W. Eckfeldt* 1888 (Mt. D); Rockland, *G. K. Merrill* (NY).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 113 in part; also *Tuckerman* in Herb.; Bald Mt., *W. G. Farlow* Sept. 1905 (H); Chocorua, *W. G. Farlow* Sept. 1907 (H); Fitzwilliam, *R. H. Howe, Jr.*, Aug. 6, 1909 (R).

VERMONT: Mt. Mansfield, *C. G. Pringle* no. 197 (BSNH); Willoughby, *G. G. Kennedy* July 28, 1898 (H).

MASSACHUSETTS: Chelmsford and Salem, *J. L. Russell* 1850 (Tuck); Concord, *R. H. Howe, Jr.* (Th); Ipswich, *Oakes* and *Tuckerman* Nov. 1842 (Tuck); New Bedford, *Willey* 1881 (Tuck).

NEW YORK: Adirondack Mts., *L. W. Riddle* Aug. 1908 (R).

This is the only species treated in this paper of which the synonymy is

confused, the uncertainty arising on account of the doubt as to what ACHARIUS meant by his *Lichen cereolus*, described in *Lichenographia Suecicae Prodromus* (1798), p. 89, and figured as *Stereocaulon cereolus* in *Methodus Lichenum* (1803), *pl. 7, fig. 1.* In TH. FRIES's *Monograph* (1858), p. 40, the treatment is confused, *S. cereolus* being placed as a variety under *S. cereolinum* (Ach.) Koerb., of which *S. pileatum* is made a synonym, apparently disregarding priority. But in his *Lichenographia Scandinavica* (1871), p. 55, TH. FRIES states that according to the original specimens in ACHARIUS' Herbarium, *Lichen cereolus* is synonymous with *Pilophorus Fibula* Th. Fr. This would leave *S. pileatum* the oldest name and the one to be adopted, as has indeed been done by TH. FRIES (*op. cit.*) and most recent authors.

*Stereocaulon pileatum* is closely allied to *S. condensatum*, with which, as indicated in the synonymy, it was at one time united by certain authors, yet the differences between the two are greater than those between *S. paschale* and *S. tomentosum*, which have been recognized as distinct since the work of ELIAS FRIES. The points of difference are as follows.

| *S. pileatum* | *S. condensatum* |
|---|---|
| 1. Squamules typically coralline. | 1. Squamules granular. |
| 2. Podetia simple and reduced. | 2. Podetia stouter, often branched above. |
| 3. Apothecia often replaced by soredia. | 3. Apothecia never replaced by soredia. |
| 4. Spores with blunt ends, and averaging 4 $\mu$ in width. | 4. Spores with pointed ends, and averaging 2.7 $\mu$ in width. |
| 5. Growing on rocks. | 5. Growing on soil. |

*S. pileatum* also shows a strong resemblance to forms of *Pilophorus*. When fertile the spore differences will of course serve for their distinction.

2. STEREOCAULON CONDENSATUM Hoffm.

*S. condensatum* Hoffm. Deutsch. Fl. 2:130. 1795.

Primary thallus persistent, formed of coarse, rounded granules, intermixed with conspicuous black masses of *Stigonema*, with which are formed dark, rugose cephalodia; podetia stout, simple or fastigiately branched above; squamules granular, rarely coralline; apothecia well developed; spores 20–28×2.5–3 $\mu$, average 23×2.6 $\mu$, with pointed ends.—Growing on soil.

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 88; Schaer. Lich. Helv. no. 509; Anzi Lich. Ital. Suppl. no. 29; Nyl. and Norrl. Herb. Lich. Fenn. no. 87.

CANADA: Labrador, *A. P. Low* July 21, 1896 (Can); Quebec, *Macoun* Aug. 11, 1905 (Can).

MASSACHUSETTS: Wellesley, *Clara E. Cummings* in Dec. N. A. L. 26; South Sudbury, *C. M. Carr* (R); Ipswich, *Wm. Oakes* (Tuck); Duxbury, *J. L. Russell* (Tuck); New Bedford, *H. Willey* (BSNH); Mattapoisett, H. *Willey* (R).

CONNECTICUT: Montville, *W. A. Setchell* (Tuck); Norwich, *W. A. Setchell* (H).

The differences which distinguish this species from *S. pileatum* are sufficiently indicated in the notes under the latter, to which reference may be made.

## Section EUSTEREOCAULON

Primary thallus soon disappearing; podetia mostly tall, well developed, and irregularly branched; squamules well developed, cartilaginous, gray or white, but never chalky.—Spores 15–35× 2.5–5 μ, with some minor variations among the species, but on the whole so uniform as to be without value in specific diagnosis.

3. STEREOCAULON CORALLOIDES Fries.

*S. coralloides* Fries Lich. Suec. no. 118. 1817; and Sched. Crit. p. 24. 1824.

*S. corallinum* Laurer in Fries Lich. Eu. p. 201. 1831.

*S. corallinum* Fries in Tuck. Syn. Lich. N.E. p. 45. 1848.

*S. Despreaultii* Delise ms. in Nyl. Syn. p. 249. 1858 (according to authentic specimen in Herb. Tuck.).

Podetia solitary or caespitose, erect, branched, usually extensively, glabrous or subtomentose; squamules coralline and branching, giving the plant a fibrillose appearance; apothecium medium to large (1–4 mm.), mostly terminal;] cephalodia of the type of *S. paschale* (*q.v.*), usually abundant and conspicuous.—Growing on rocks (fig. 5).

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 118; Stenh. Lich. Suec. no. 82; Sweden, *Th. Fries*, Leighton Collection (NY), also *Nylander* (*loc. cit.*); Schaer. Lich. Helv. no. 261; Hepp Lich. Eu. no. 114; Pyrenees, *R. Spruce* in Leighton Collection (NY).

BRITISH AMERICA: Labrador, *Townsend* July 1906 (H); Newfoundland, *Waghorne* no. 46, no. 66 as *S. tomentosum*, no. 67 as *S. paschale* (CEC); New Brunswick, *Farlow* July 1892 (H); *Willey* (Tuck); Cape Breton Is., *Macoun* July 22, 1898 (Can); Nova Scotia, *A. H. Mackay* (BSNH); Ontario, *Macoun* (Can); Lake Superior, *Macoun* (Can); Vancouver Is., *Macoun* (Can); *Calder* (BSNH); *Lyall* (Tuck).

ALASKA: Unalaska, *J. M. Macoun* June 4, 1897 (Can); St. Paul Is., *J. M. Macoun* June 19, 1897 (Can).

MAINE: Eastport, *Farlow* (H); West Pembroke, *Maude C. Wiegand* Aug. 11, 1909 (W); Mt. Katahdin, *J. F. Collins* in Herb.; Mt. Desert Is., *M. L. Wilson* (Mt. D).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 94; *E. Faxon*, as *S. denudatum* (CEC); *Clara E. Cummings* (R); *Farlow* (H).

VERMONT: Brattleboro, *C. C. Frost* (UVM).

NORTH CAROLINA: *Buckley* (NY); *J. W. Harshberger* (NY).

A beautiful species, entirely distinct from all others of the boreal group in the coralline or fibrillose squamules (fig. 8), clearly separating it from *S. paschale* and *S. tomentosum*, which it resembles in habit. Although much the rarest of the three species, it is nevertheless rather remarkable that no specimens have been seen from the central or western parts of the United States.

4. STEREOCAULON PASCHALE (L.) Ach.

*Lichen paschalis* Linnaeus Sp. Pl. **2**:1153. 1753 (cf. WAINIO *Revisio lichenum in herbario Linneai asservatorum* in Medd. Soc. F. et Fl. Fenn. **14**:1. 1886).

*Stereocaulon paschale* Acharius Meth. Lich. p. 315. 1803, in part (cf. TH. FRIES Monog. Ster. p. 58).

*Stereocaulon paschale* Fries emend. in Lich. Eu. p. 202. 1831.

Podetia 3 to 9 cm. high (average 6 cm.), caespitose, lax, spreading, procumbent, or rarely erect, more or less intricately branched throughout, glabrous or somewhat tomentose; squamules palmate-digitate, or margin crenate, or, on upper part of podetia, granulate, never coralline; apothecia 0.5 to 4 mm. in diameter, average 1 mm., terminal or terminal and lateral; cephalodia typically conspicuous, gray, spherical, rugose-plicate, containing *Stigonema*, sometimes fibrillose and black.—Growing on rocks, rarely on the earth.

SPECIMENS EXAMINED

EUROPE: Stenh. Lich. Suec. no. 80; Sweden, *Th. Fries* 1854, and *Tuckerman* 1842 (Tuck).

BRITISH AMERICA: Labrador, *A. P. Low* July 1896 (Can); *Waghorne*, Aug. 1891 (NY); Quebec, Gaspe County, *J. F. Collins* July 19, 1906 (R); New Brunswick, *G. U. Hay* July 1884 (Can); Nova Scotia, *Mackay* (BSNH); Ontario, many localities, *Macoun* (Can); Lake Superior, *Macoun* Canad. Lich. no. 45; Alberta, *H. L. Bolley* Aug. 1901 (F); British Columbia, *Macoun* (Can).

ALASKA: *J. M. Macoun* 1892 (Can); Sheep Creek near Juneau, *Grace E. Cooley* Aug. 5, 1891, as *S. tomentosum* (CEC); Muir Glacier, *Trelease* June 9, 1899, Harriman Exped. no. 1299, as *S. tomentosum* (CEC); Port Cla en ,

Behring Strait, *Trelease* July 12, 1899, Harriman Exped. no. 1266, as *S. tomentosum* (CEC).

MAINE: Eastport, *W. G. Farlow* 1877 (Tuck); Portage, *L. W. Riddle* Aug. 1907 (R); Rangeley *L. W. Riddle* Aug. 1904 (R); Orono, *L. W. Riddle* July 1907 (R); Mt. Desert, *M. L. Wilson* (Mt. D), *Sam Surrey* (R); Rockport, *G. K. Merrill* Lich. Exs. no. 40; Cumberland, *J. Blake* (NY).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 122; North Woodstock, *Clara E. Cummings* in N. A. L. no. 25, L. B. A. no. 151; Crawfords, *Miss Minns* (W); Warren, *Charles W. Riddle* Aug. 1908 (R); Mt. Chocorua, *H. H. Bartlett* Sept. 1906 (R); Mt. Monadnock, *W. G. Farlow* (H); *R. H. Howe, Jr.* (Th); Fitzwilliam, *R. H. Howe, Jr.*, Lich. Nov. Ang. no. 22.

VERMONT: Mt. Mansfield, *C. G. Pringle* 1879 (UVM); Willoughby, *W. G. Farlow* (H); Bristol, *L. W. Riddle* Aug. 12, 1908 (R).

MASSACHUSETTS: Pepperell, *L. W. Riddle* May 30, 1909 (R); Mt. Watatic and Concord, *R. H. Howe, Jr.* (Th); Arlington, *B. Fink* May 1895 (R); "near Boston," *T. P. Adams* (BSNH).

CONNECTICUT: Woodbridge, *G. E. Nichols* March 13, 1909 (R).

NEW YORK: Adirondack Mts., *Mrs. C. W. Harris* 1900 (R); *L. W. Riddle* Aug. 1908 (R).

OHIO: *Lesquereux?* (NY).

MICHIGAN: *E. T. Harper* Aug. 1899 (R).

WISCONSIN: *C. F. Baker* (CEC).

MINNESOTA: *Macmillan* 1894 (R); *B. Fink* July 30, 1902 (R).

OREGON: *E. Hall* 1871 (Tuck).

TUCKERMAN, following TH. FRIES, cites E. FRIES as the author of this species. The combination was first made, however, by ACHARIUS (*op. cit.*), who refers to the figure in *English botany, pl. 282*. According to the Vienna Code (Articles 40 and 41), ACHARIUS should be cited therefore as the author, even though his conception of the species was later emended by FRIES through the segregation of *S. tomentosum* and *S. coralloides*.

*S. paschale* is the commonest and most widely distributed species of the genus, at least in the eastern portion of North America. In the west it seems to be comparatively rare, its place being taken by *S. tomentosum*.

The two species named may be best separated from their allies by the palmate-digitate type of squamules (fig. 7). The chief difficulty, however, comes in finding satisfactory characters to distinguish *S. paschale* from *S. tomentosum*. Typical *S. paschale* is said to have glabrous podetia, while in *S. tomentosum* they are said to be densely tomentose. But a study of a sufficient amount of material shows that there are all gradations from wholly glabrous podetia through a medium amount of tomentum to densely tomentose. As the tomentum is the chief character hitherto used as diagnostic, it is clear that with such variability much confusion must result. A second character which has been used is the position of the apothecia, in typical *S. paschale*

the apothecia being at least in part terminal, while in *S. tomentosum* they are said to be always lateral. Here again we have a variable character which cannot be used as a precise criterion.

In searching for a character which would by its nature be mutually exclusive for the two species, the attempt was made to use the cephalodia. The differences between the cephalodia typical of these two species are sufficiently indicated in the descriptions, to which reference may be made. To establish the taxonomic value of this structure, it was necessary to prove three points: first, both types of cephalodia must not occur on the same plant; secondly, the cephalodia must be constant enough in occurrence to be of use; and thirdly, the characteristics of the cephalodia must be correlated with the other diagnostic characters.

As has been shown by various investigators, the cephalodia of lichens are peculiar gall-like outgrowths formed by the hyphae of the thallus surrounding some foreign alga. A priori we should hardly expect that such a structure would be constant enough to be used in classification. The method adopted to prove the points mentioned was to make a statistical study of a large number of specimens of the *paschale-tomentosum* group, noting the type of cephalodium, the amount of tomentum, and the position of the apothecia, and then to tabulate the results. In this statistical study material was examined from various parts of North America and Europe, and the specimens were taken as they came in the herbaria, in order to avoid influencing the results by conscious choice. The only exception was made in the case of a few specimens which were so clearly depauperate that they could in no way be looked upon as aiding in the object sought. The results are given in the following tables:

| | |
|---|---|
| Number of specimens examined | 103 |
| Specimens with both types of cephalodia | 1 |
| Specimens lacking cephalodia | 9 |
| Specimens lacking apothecia | 22 |

The fact that on only one specimen studied were both types of cephalodia found shows that for practical purposes the two types are mutually exclusive. Cephalodia being present in a larger proportion of specimens than were apothecia, it follows that if apothecial characters or spore characters are of value cephalodia can equally well be used, as far as constancy of occurrence is concerned. To show correlation of characters, the results may be arranged as follows:

| Cephalodia | Apothecia | | |
|---|---|---|---|
| | Terminal | Mixed | Lateral |
| *Tomentosum* type | 1 | 13 | 28 |
| *Paschale* type | 11 | 18 | 3 |

| Cephalodia | Tomentum | | |
|---|---|---|---|
| | Absent | Medium | Abundant |
| *Tomentosum* type.... | 0 | 16 | 34 |
| *Paschale* type..... | 24 | 19 | 0 |

These tables show conclusively the extent to which *S. paschale* and *S. tomentosum* intergrade. They show also the confusion introduced by taking the presence of tomentum alone as a criterion, for, as is shown in the second table, out of 93 specimens 35 were intermediate in the amount of tomentum. With such intergrading, complete correlation of characters is not to be expected. But the tables show that the types of cephalodia are correlated to a marked degree with the two characters that have been recognized as of chief importance in separating these two species. The results of the statistical study, therefore, support very strongly the suggestion that the cephalodia, when present, are of great taxonomic value. Yet taking all available characters into consideration, there are still specimens which cannot be placed absolutely under either of these species, but exhibit characters of both. And this must necessarily be so on account of the fact that in nature *S. paschale* and *S. tomentosum* evidently form a continuous, variable series, the forms that we recognize as "typical" being merely the two extremes of this series.

Of the numerous forms of *S. paschale* which have been distinguished by European authors only one seems to be of sufficient importance in North America to receive separate treatment. This is

4*a*. Stereocaulon paschale var. conglomeratum Fries.

Fries Sched. Crit. ad Lich. Suec. **3**:20. 1824.

Podetia much branched, forming compact cushions which are closely adnate to the substratum, squamules more granular and crowded than in the type; usually sterile.—Growing on rocks.

SPECIMENS EXAMINED

Europe: Fries Lich. Suec. no. 89; Hepp Lich. Eu. no. 304; Sweden, *Areschoug* (Tuck).

New Hampshire: Mt. Monadnock, *W. G. Farlow* July 1, 1896 (H); Alton Bay, *C. J. Sprague* (BSNH).

Vermont: Mt. Ascutney, *R. H. Howe, Jr.*, Aug. 25, 1909 (Th).

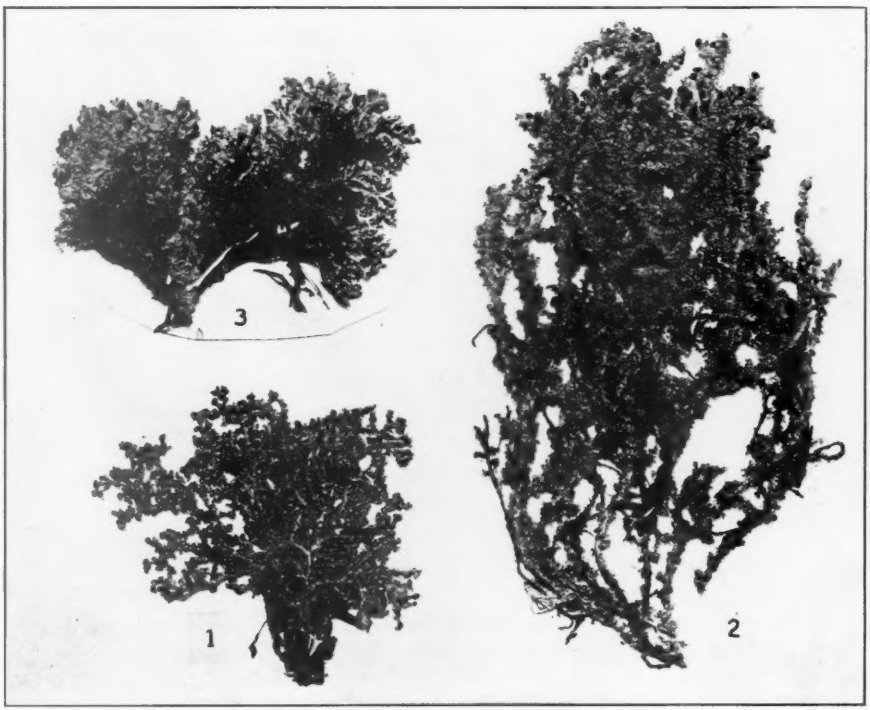
Massachusetts: Annisquam, *Clara E. Cummings* 1892 (CEC); Wellesley, *Clara E. Cummings* Dec. 1884 (CEC); *L. W. Riddle* Jan. 1908 (R).

This is a reduced form of *S. paschale*, occurring either at low altitudes or on rocks with extreme exposure. It passes into the laxer, more typical form by insensible gradations. The only other species with which this variety may

be confused is *S. denudatum*, and the specimens from Ipswich, Mass. (*Wm. Oakes*), and from Nantasket, Mass. (*H. Willey*), in the Tuckerman Herbarium, labeled *denudatum*, seem to be much nearer this variety of *S. paschale*. The two have a general resemblance in habit, but *S. paschale* var. *conglomeratum* is less denuded and always has indications of the palmate-digitate type of squamules typical of *S. paschale*.

5. STEREOCAULON TOMENTOSUM Fries.

*S. tomentosum* Fries Sched. Crit. ad Lich. Suec. 3: 20. 1824.




FIGS. 1, 2, 3.—Fig. 1, *Stereocaulon tomentosum* Fr., typical form; specimen from Disenchantment Bay, Alaska, collected by W. TRELEASE, June 19, 1899, Harriman Exped. no. 1297, in herbarium of CLARA E. CUMMINGS; photo. nat. size; fig. 2, *Stereocaulon tomentosum* Fr., large form; specimen from Cascade Mts., Oregon, collected by C. G. PRINGLE, Sept. 20, 1881, in herbarium of Wellesley College; photo. nat. size; fig. 3, *Stereocaulon Wrightii* Tuck.; specimen from St. Michael, Alaska, collected by W. A. SETCHELL, University of California Expedition, 1899, in herbarium of CLARA E. CUMMINGS; photo. nat. size.

Podetia loosely attached to the substratum, erect, or spreading, 3 to 9 cm. high, average 5 cm., more or less densely tomentose; squamules palmate-digitate, abundant, more or less crowded; apothecia typically minute, 0.5 to 1 mm. in diameter, rarely larger, reaching 2 mm., lateral; cephalodia minute, verdigris-green, containing *Nostoc*.—Growing on the ground or among mosses, rarely on rocks (fig. 1).

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 90; Stenh. Lich. Suec. no. 79; Hepp Lich. Eu. no. 302; Rabenh. Lich. Eu. no. 133; Lojka Lich. Hungarici no. dh; Upsala, *Th. Fries* 1854 (Tuck); Sweden, *Nylander* in Leighton Coll. (NY).

BRITISH AMERICA: Labrador, *Waghorne* no. 33, as *S. denudatum* (CEC); Anticosti, *Macoun* Aug. 22, 1883 (Can); New Brunswick, *G. U. Hay* June 24, 1882 (Can); Gaspe County, Quebec, *Macoun* July 28, 1882 (Can); *J. F. Collins* Aug. 17, 1906 (R); Cape Breton Is., *Macoun* July 9, 1898 (Can); Nova Scotia, *Macoun* June 12, 1883 (Can); Great Bear Lake, *Richardson* (H); Lake Superior, *Macoun* July 29, 1869 (Can); *Agassiz* 1848 (Tuck); British Columbia, many localities, *Macoun* (Can); *G. Dawson* Oct. 5, 1888 (Can); Alberta, *Macoun* June 13, 1907 (Can); *L. R. Waldron* June 16, 1901 (F).

ALASKA: *Dr. Kellogg* (Tuck); *P. M. Newhall* on Univ. Calif. Exped. 1899 (CEC); *Trelease* in Harriman Exped. nos. 1267, 1297, 1300, 1301; *Coville* and *Kearney* in Harriman Exped. nos. 609, 981, 2121 (CEC).

MAINE: Eastport, *Farlow* (H); Mt. Desert, *M. L. Fernald* Sept. 18, 1892 (CEC); Cumberland, *J. Blake* Dec. 1855 (CEC).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 23; Crawfords, *Miss Minns* (W); North Woodstock, *Clara E. Cummings* Aug. 19, 1892 (CEC); Shelburne, *Farlow* Aug. 1894 (H); Fitzwilliam, *R. H. Howe, Jr.* (Th.)

VERMONT: Hinesburgh, *C. G. Pringle* 1878 (UVM); Brattleboro, *C. C. Frost* (UVM).

MASSACHUSETTS: Magnolia, *C. J. Sprague*, as *S. paschale* (BSNH); Duxbury, *J. L. Russell* (B); New Bedford, *H. Willey* (B).

CONNECTICUT: Ellsworth, *H. A. Green* Aug. 7, 1887 (NY).

NEW YORK: *C. F. Austin* (NY); *E. A. Burt* (F); *K. M. Wiegand* (W); *L. W. Riddle* (R).

ILLINOIS: *J. Wolf* 1888 (NY).

MINNESOTA: Various localities, *B. Fink*, in Herb.; *Macmillan* (F).

COLORADO: *T. S. Brandegee* (R); *F. E. Clements*, as *S. paschale* (H).

MONTANA: *T. A. Williams* in Dec. N. A. L. no. 292.

WYOMING: *Aven Nelson* no. 2690 (NY).

WASHINGTON: *W. W. Calkins* no. 340, as *S. paschale* (W); Puget Sound *B. Fink* June 30, 1906 (F); Longmire's Springs, *E. T. Harper* Aug. 1906 (F).

OREGON: *C. G. Pringle* Sept. 20, 1881 (W); *E. Hall* 1871 (H); *J. W. Eckfeldt* 1882 (Can).

The relationship of *S. tomentosum* to *S. paschale* is sufficiently discussed under the latter species, to which reference may be made. The palmate-digitate type of squamules will serve to distinguish these species from others having the same habit, including *S. alpinum*, our only other species with typically tomentose podetia.

Certain material has been examined from our northwest coast, especially from the Cascade Mts., Oregon, which seemed at first to be distinct from *S. tomentosum* (fig. 2). These specimens are unusually large and finely developed, with large apothecia, and bearing conspicuous white structures which at first appeared to be a new type of cephalodium. Examination of these structures failed to show any type of alga other than the *Cystococcus*, which forms the normal gonidia for the genus, and the structures cannot therefore be considered cephalodia. After careful study I am unable to look upon this Oregon material as anything more than exceptionally luxuriant *S. tomentosum*.

It is otherwise, however, with another form of *S. tomentosum*, which is undoubtedly of varietal rank and may be designated

5*a*. STEREOCAULON TOMENTOSUM var. **simplex,** var. nov.

Podetia 6–9 cm. alta, erecta, simplicia vel subsimplicia; squamulae paucae et dispersae; tomentum et apothecia et cephalodia ut in forma typica.—Habitat in locis arenosis.

Podetia 6–9 cm., tall, erect, simple or nearly so; squamules few and scattered; tomentum, apothecia, and cephalodia as in the type.—Growing in bare sandy soil (fig. 4).

Type specimens: "On sandy river bottom, Mt. Rainier region, Washington," collected by *T. C. Frye*, Aug. 14, 1904, in Herb. L. W. Riddle.

Co-type specimens: in Herb. Fink and Herb. Wellesley College.

SPECIMENS EXAMINED

OREGON: Cascade Mts., *Moses Craig* Aug. 1898 (CEC), *A. S. Foster* June 20, 1907 (R).

WASHINGTON: Mt. Rainier region *T. C. Frye* Aug. 15, 1904 (R); Olympic Mts., *T. C. Frye* Aug. 7, 1907 (R).

BRITISH COLUMBIA: Salt Spring Is. Gulf of Georgia, *Macoun* May 9, 1887 (Can).

ALASKA: Davidson Glacier, *Grace E. Cooley* Aug. 15, 1891 (CEC).

This variety is very striking and distinct, and can scarcely be confused with any other North American form.

6. STEREOCAULON ALPINUM Laurer.

*S. alpinum* Laurer in Fries Lich. Eu. p. 204. 1831.

*S. tomentosum* var. *alpinum* (Laur.) Th. Fr. Comm. Ster. p. 30. 1857, and American authors.

FIGS. 4, 5, 6.—Fig. 4, *Stereocaulon tomentosum* var. *simplex* Riddle; type specimens from Mt. Rainier region, Washington, collected by T. C. FRYE, Aug. 14, 1904, in herbarium of L. W. RIDDLE; photo. nat. size; fig. 5, *Stereocaulon coralloides* Fr.; specimen from the Austrian Tyrol, collected by KERNSTOCK and issued in *Kryptogammae Exsiccati* (Vienna), no. 355, herbarium of L. W. RIDDLE; photo. nat. size; fig. 6, *Stereocaulon denudatum* Floerke; specimen with the granulate type of squamules, from Minnesota, collected by BRUCE FINK, June 19, 1897, in herbarium of L. W. RIDDLE; photo. nat. size.

Podetia stout, erect, 1 to 6 cm. tall, more or less densely branched, and tomentose; squamules in the form of coarse, crowded, conglomerate granules; apothecia (rare) medium to large, lateral or terminal; cephalodia of the type of *S. tomentosum* (*q.v.*).—Growing on exposed soil, especially in arctic-alpine regions.

SPECIMENS EXAMINED

EUROPE: Authentic specimens ex Herb. Laurer (F); Schaer. Lich. Helv. no. 263; Massalongo Lich. Ital. no. 11; Anzi Lich. Ital. Suppl. no. 26; Rabenh. Lich. Eu. no. 859; Arnold Lich. Exs. 5 no. 641*a;* Finmark, *Th. Fries* (Tuck).

BRITISH AMERICA: Greenland, *Fink* (NY); Cumberland Is., *Howgate Exped.* 1877 (Tuck); Diggs Is. Husdon Bay, *R. Bell* (Can); Labrador, *Waghorne* no. 20, also no. 21 as *S. condensatum* (CEC); *A. P. Low* (Can); Alberta, *Macoun* June 28, 1905 (Can).

ALASKA: St. Paul Is., *T. C. Kincaid* (F); Is. in Behring Strait, *C. Wright* (Tuck); Port Foulke, *Dr. Hayes* (Tuck); *Fred Funston* 1894 (CEC); *Trelease* in Harriman Exped. nos. 1268, 1270, 1298*a* (CEC); *Dall* in Harriman Exped. no. 1295, as *S. tomentosum* (CEC).

MAINE: Eastport, *Farlow* (H); Portage *L. W. Riddle* Aug. 1907 (R).

NEW HAMPSHIRE: Mt. Washington, *Farlow* Sept. 1894 (H).

MINNESOTA: *B. Fink* no. 93 (F).

OREGON: Mt. Hood, *E. Hall* 1871 (Tuck).

WASHINGTON: Mt. Rainier, *C. V. Piper* 1895 (CEC); Friday Harbor, *B. Fink* June 28, 1906 (F).

This is clearly distinct as a species from *S. tomentosum*, as the type of squamules is a specific criterion throughout the genus. It is most liable to confusion with *S. denudatum* which it resembles in general habit and range, but it can be distinguished by the tomentum and the type of cephalodium.

7. STREOCAULON DENUDATUM Floerke.

*S. denudatum* Flke. Deutsch. Lich. **4**:13. 1819.

*S. glaubescens* Tuck. Bost. Journ. Nat. Hist. **3**:302. 1840 (according to original specimen).

Podetia 2 to 4 cm. high, solitary or aggregated, shrubby-erect, subsimple below, branching above, wholly glabrous, denuded below, squamulose above; squamules crowded, in the typical form umbilicate, attached by the center, and with the margin crenate (see fig. 9), or often in the form of coarse, rounded, conglomerate granules; apothecia rare in North American specimens; cephalodia of the type of *S. paschale* (*q.v.*).—Growing on exposed rocks or soil (fig. 8).

SPECIMENS EXAMINED

EUROPE: Authentic specimen ex Herb. Floerke in Herb. Tuck.; Fries Lich. Suec. no. 346; Arnold Lich. Exs. no. 1576; Sweden, *Forssell* 1880 (NY); Scotland, *Leighton* July 1869 (NY); France, *L. Breviere* (R).

BRITISH AMERICA: Greenland, *Eberlin* 1885 (Can); *Warming* and *Holm* 1884 (H); Kikkeston Is., *Howgate Exped.* 1877 (Tuck); Hudson's Strait, *R. Bell* 1884 (Can); Labrador, *Wm. Palmer* 1887 (NY); *Owen Bryant* Aug. 22, 1908 (H); Newfoundland, no collector given (BSNH); *Delise* (Tuck) not typical.

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 114; Mt. Washington, *W. G. Farlow* Sept. 1891 (H); Mt. Adams, *W. G. Farlow* Sept. 1897 (H); Mt. Willard, *E. Faxon* June 1882 (CEC); Mt. Monadnock, *W. G. Farlow* July 1896 (H).

VERMONT: *C. C. Frost* (BSNH); Mt. Mansfield, *W. G. Farlow* Sept. 1890 (H).

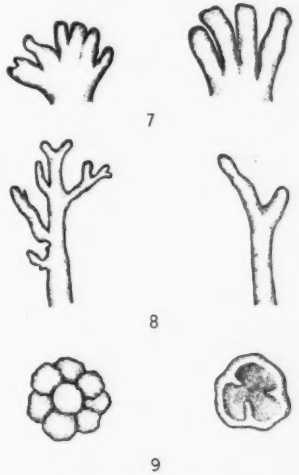
NEW YORK: *Mrs. C. W. Harris* June 1900 (R); Adirondack Mts., *W. G. Farlow* Sept. 1902 (H).

MASSACHUSETTS: Mt. Holyoke, *Whitman* May 20, 1839 (Tuck).

MINNESOTA: *B. Fink* no. 49 in Herb.

WASHINGTON: *Suksdorf* (BSNH).

CALIFORNIA: *Bolander* in Herb. Tuck. (doubtful!).



FIGS. 7, 8, 9.—Fig. 7, palmate-digitate type of squamules found in *S. paschale* and *S. tomentosum;* enlarged; fig. 8, typical squamules of *S. coralloides;* enlarged; fig. 9, squamules of *S. denudatum;* right, umbilicate type; left, granular type; enlarged and semi-diagrammatic.

ALASKA: *Dr. Kellogg* 1867 (Tuck); *W. A. Setchell,* Univ. Calif. Exped. 1899 (CEC); *W. H. Evans* 1897, as *S. alpinum* (CEC); *Harriman Exped.* no. 1279, as *S. alpinum* (CEC).

The two types of squamules described for this species intergrade, and the granulate type is scarcely worthy of varietal rank. The typical umbilicate squamules are found in specimens from arctic or subarctic stations. When these are present there should be no difficulty in distinguishing *S. denudatum* from all other species. But specimens with the coarsely granular squamules are less distinctive, and are frequently mistaken for either *S. paschale* or *S. alpinum.* From the latter the wholly glabrous podetia and the type of cephalodia should serve to distinguish *S. denudatum;* while the error of mistaking it for *S. paschale* may be avoided if it is borne in mind that in true *S. paschale*

some indication of the characteristic palmate-digitate type of squamules is always to be seen, and this type is never to be found in *S. denudatum*.

The most puzzling specimens that I have seen are those collected in New Jersey by C. F. AUSTIN. Portions of this material have been examined in the Tuckerman Herbarium, the Sprague Collection at the Boston Society of Natural History, and the Herbarium of the New York Botanical Gardens. It was determined by TUCKERMAN as *S. denudatum*, and is cited in his *Synopsis of North American Lichens*, p. 233; yet it is scarcely typical of this species, and it seems much nearer to *S. paschale*, a view which would be supported by the latitude of the station, *S. denudatum* being essentially an arctic-alpine species.

According to the description of this species given by TH. FRIES, the apothecia are minute (i.e. about 0.5 mm. in diameter) and lateral. But the specimen collected by C. C. FROST in Vermont and now in the Sprague Collection (BSNH), agreeing in all other particulars with *S. denudatum*, has terminal apothecia, over 1.5 mm. in diameter.

8. STEREOCAULON WRIGHTII Tuck.

*S. Wrightii* Tuck. Suppl. II to Enum. N. Am. Lich. in Am. Journ. Sci. **28**:202. 1859.

*Stereocladium Wrightii* Nyl. Lich. Freti Behr. p. 85. 1888.

*Stereocaulon foliiforme* Hue Bull. Soc. Bot. France **54**:414. 1907 (see below).

Podetia 1 to 4 cm. tall, solitary or caespitose, branched above, wholly glabrous, denuded below, ending in broad, foliose, convolute tips, taking the place of the usual squamules; or the podetia reduced and the expanded portions alone present; apothecia unknown; cephalodia doubtful (fig. 3).

Hitherto this species has been known only from the type collection made by CHARLES WRIGHT at Arakamtchetchene Is. on the Asiatic side of Behring Strait, during the U.S. North Pacific Exploring Expedition (1853–1856). To this may now be added two other localities, from both of which specimens have been distributed under other names. A comparison of these specimens, however, with the type specimens of *S. Wrightii* in the Tuckerman Herbarium shows that they are undoubtedly this species. These specimens are from St. Michael, Alaska, collected by W. A. SETCHELL on the University of California Expedition in 1899, and distributed as *Stereocaulon denudatum;* and from Shiribeshi, Japan, collected by ABBE FAURIE, July 1905, and issued in Faurie Lich. Jap. no. 6999 as *Stereocaulon foliiforme* Hue, n. sp.; an authentic specimen determined by HUE himself is in the herbarium of W. G. FARLOW.

Section CHONDROCAULON (*Leprocaulon* Nyl.)

Primary thallus present or disappearing; podetia reduced, simple or branched; squamules granular, dissolving into chalky-white powder.

9. STEREOCAULON ALBICANS Th. Fr.

*S. albicans* Th. Fr. Comm. Ster. p. 36. 1857.

*S. tenellum* Tuck. Bot. Wilkes Voy. p. 123. 1861 (according to type specimens).

Podetia short, mostly under 1 cm., slender, caespitose, branched, crowded and intertangled; squamules minutely granular, becoming powdery; apothecia unknown.—The whole plant is characteristically chalky-white and powdery.

SPECIMENS EXAMINED

NORTH AMERICA: Greenland, Kikkeston Is., *Howgate Exped.* 1877 (Tuck); Vancouver Is., *Macoun* May 19, 1893 (Can); Colorado, *T. S. Brandegee* (BSNH); Arizona, Rincon Mts. near Tucson, *J. C. Blumer* Oct. 1909 (R); California, *C. R. Orcutt* (BSNH); *W. G. Farlow* (H); Guadeloupe Is., *E. Palmer* 1875 (Tuck); Cuba, *C. Wright* (Tuck).

SOUTH AMERICA: New Granada, *Lindig* no. 2502 (Tuck); Peru, *Wilkes Exped.* (Tuck), type of *S. tenellum* Tuck.

This is a rare and interesting species, first described by TH. FRIES from material collected by GAUDICHAUD in Peru, but with a wide distribution as indicated. It is the representative in the western hemisphere of the Old World *S. nanum* Ach. It does not resemble any other American species sufficiently to cause confusion.

DOUBTFUL SPECIES

*Stereocaulon nanodes* Tuck. in Suppl. II to Enum. N. A. Lichens, Am. Jour. Sci. **28**:201. 1850.

Primary thallus absent; podetia about 1 cm. tall, dendroid-branched, glabrous, more or less denuded; squamules in the form of small rounded granules, dissolving into fine, whitish powder (but not chalky as in *S. nanum*); apothecia terminal, or absent and the podetia ending in masses of soredia as *S. pileatum*.—Spores 24–42×2.5–3 μ.

I have examined at the Tuckerman Herbarium the type specimens of this species, collected by TUCKERMAN at Crystal Falls, Saco Falls, and upper gorge of the Ammonoosuck, in the White Mts., New Hampshire. Although not readily referable to any other species of *Stereocaulon*, I have placed this species as doubtful on account of the fact that it has apparently never been collected again in the White Mts., which is perhaps one of the most thoroughly explored regions, botanically, in North America. The only other record of this species is Newfoundland on the authority of Dr. J. W. ECKFELDT. Through the courtesy of Mr. WITMER STONE of the Philadelphia Academy of Sciences I

have had an opportunity to examine the specimens upon which this record was based. One sheet is *S. pileatum* Ach.; the other, depauperate specimens of *Cladonia decorticata* (Flke.) Spreng. The species is known, therefore, only from the type collections.

*Stereocaulon ramulosum* (Sw.) Ach.

In the herbarium of the Geological Survey of Canada is a sheet bearing three specimens of this species with the label: "Lichenes Boreali Americani. No. 89. Dalles, Oregon, on the earth. Legi John W. Eckfeldt. 1880." As no corresponding specimens are to be found in Dr. ECKFELDT's herbarium at the Philadelphia Academy of Sciences, and as *S. ramulosum* is not otherwise known from the United States, there has undoubtedly been some mistake in the labeling of the specimens mentioned above.

WELLESLEY COLLEGE
WELLESLEY, MASS.

# BRIEFER ARTICLES

## THE EPIDERMAL CHARACTERS OF FRENELOPSIS RAMOSISSIMA

(WITH TWO FIGURES)

The genus *Frenelopsis* was founded by SCHENCK in 1869[1] upon abundant material from the Wernsdorferschichten (Lower Cretaceous), and named from its resemblance to the modern genus *Frenela*. *Thuites Hoheneggeri* of ETTINGSHAUSEN was the type and only species. This was, he says, the most abundant fossil in those beds in which it occurs, and it received a careful and elaborate treatment at his hands. This species has subsequently been recognized in the Kome beds of Greenland, the Trinity beds of the Texas region, the Raritan and Magothy formations of New Jersey, and the Turonian of Bagnols, France. In 1880 HOSIUS and VAN DER MARCK described a rather illy defined species, *Frenelopsis Königii*, from the Senonian of Westphalia,[2] and the next year HEER[3] described an additional species, *F. occidentalis*, from Portugal, which SAPORTA has shown[4] ranges from the Urgonian of Cercal, through the Albian of Nazareth, into the Cenomanian of Alcantara and Padrao. The latter author also describes an additional species, *F. leptoclada*,[5] which is confined to the Lower Cretaceous of Portugal (Neocomian-Aptian).

In 1889 VELENOVSKY described the Bohemian form *F. bohemica* from the Cenomanian of that country (*op. cit.*), and the next year FONTAINE described the two species *F. ramosissima* and *F. parceramosa* from the Potomac group of Virginia, the same author three years later founding a third species, *F. varians*, upon material from the Trinity group of Texas. NEWBERRY in 1896 described a ninth species, *F. gracilis*,[6]

[1] Palaeontographica **19**:13. 1869.

[2] *Ibid.* **26**:132, 181. *pl. 37, fig. 148.* 1880.

[3] Cont. Foss. Fl. Port. 1881:21. *pl. 12, figs. 3b, 4–7.*

[4] Fl. Foss. Port. 1894:139, 199, 214. *pl. 26, fig. 16; pl. 36, figs. 1, 2; pl. 38, figs. 2, 3; pl. 39, fig. 20.*

[5] *Ibid.* 109, 113. *pl. 19, fig. 18; pl. 21, figs. 9–11.*

[6] Fl. Amboy Clays 1896:59. *pl. 12, figs. 1–3a.*

which is a very abundant Upper Cretaceous type, and which has been recently shown by HOLLICK and JEFFREY to be unrelated to *Frenelopsis*.[7]

Although fruiting specimens have not been found, the position of the genus in the Cupressineae is not disputed at the present time, although at one time HEER argued for an affinity with *Ephedra*. The genus may be defined as follows:

Shrubs or trees with cylindrical, jointed, monopodial stems and branches, the latter of which may be alternate, apparently in a single plane, or whorl, often of large size, stems up to 5 cm. in diameter having been found in the Virginia area. Leaves much reduced, somewhat variable in outline, in general triangular with a broad base and an acute apex, squamiform, appressed, one to four at the nodes, decussate. Internodes variable in length, but longer in the apparently annual shoots, which were more or less deciduous and functioned as leaves, since the fine longitudinal striae with which their surface is ornamented turn out to be rows of stomata in certain of the species which have been examined microscopically.

It is for the purpose of describing the latter characters of this interesting American Lower Cretaceous species that the following brief note is published.

*Frenelopsis ramosissima* ranges from the bottom to the top of the Lower Cretaceous in the Maryland-Virginia region to which it is thus far confined. It is by far the most abundant form at the celebrated plant locality of Fredericksburg, Va. The coarse arkosic sandy clays of this age are sometimes packed with the remains of this species, with its crowded twigs and short internodes generally completely flattened, and with all of the tissues gone except the epidermis, which must have been very tough and coriaceous in life, since the preservation of these forms was largely due to its resistant nature. The cuticle of the type of the genus, *F. Hoheneggeri*, was studied by ZEILLER and described in 1882,[8] and six years later VELENOVSKY described[9] the epidermal features of *F. bohemica*. The stomata in these species were found to consist of usually four cells, although sometimes five or even six were present. These guard cells are symmetrically arranged, the opening between them being approximately in the form of a narrow-rayed star. According to the former author, they ally these forms with the existing species of *Cal-*

[7] Mem. N.Y. Bot. Gard. **23**:6. 1909.

[8] Obs. sur quelques cuticules fossiles. Ann. Sci. Nat. Bot. VI. **13**:231. *pl. 11.* 1882; Eléments de paléobotanique 274. *fig. 196.* 1900.

[9] Ueber einige neue Pflanzenformen der böhmischen Kreideformation. Sitz. K. Böhm. Gesell. Wiss. Prag 1888:590. *figs. 1–3, 10.*

*litris* and *Libocedrus*, and effectually disprove HEER'S contention that this curious genus is a member of the Gnetales allied to *Ephedra*.

In *F. ramosissima* we find a very similar arrangement to that described in the two species just mentioned. The epidermal cells are very small, the largest not exceeding 0.025 mm. in diameter, and the average being about half this size. They are roughly rectangular in shape and have very thick walls. Their most curious feature, one not observed in any

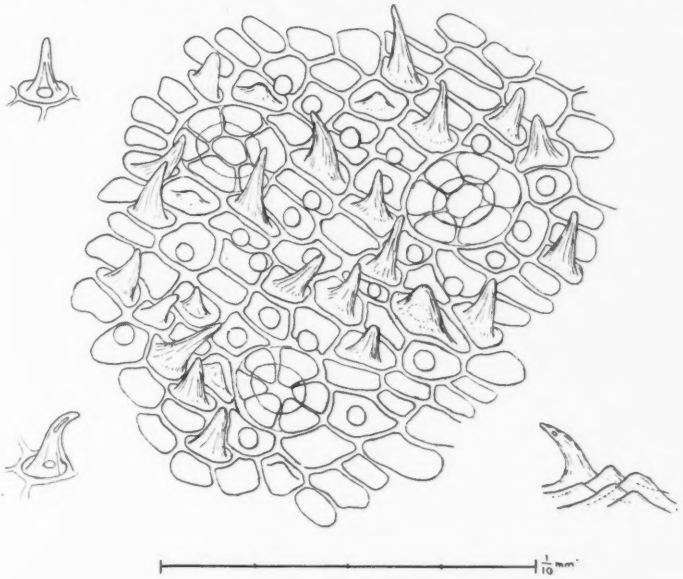



FIG. 1

other species of this genus, is the presence of minute, usually curved, spinelike outgrowths of large numbers of the epidermal cells. These protuberances vary in prominence from blunt papillae of various heights to pointed spines 0.025 mm. in length. These are not present on all of the epidermal cells, and some preparations of the epidermis are apparently entirely smooth. Fig. 1 shows a characteristic bit of the epidermis dotted with these spines. For the camera lucida drawings from which this figure was made I am indebted to Dr. FREDERICK H. BLODGETT, a former student of the Johns Hopkins University. Some of the spines, probably all of them, have a central cavity opening into the interior of the epidermal cell, which they surmount, as is shown in

one of the individual spines figured. The second and third single spines figured show irregular cavities toward the apex which are apparently cut off from the cell cavity, and the third spine figured gives a good idea of the papillose character of those adjacent cells in which these processes are not prominently developed.

In the area included in fig. 1 are three of the curious stomatal openings which apparently characterize the genus *Frenelopsis*. These are circular in outline and about 0.03 mm. in diameter. They are very numerous, but whether they are localized on certain portions of the branches which perform the functions of leaves in this genus, or whether they are uniformly distributed on the annual shoots, could not be determined. They consist of five or six guard cells arranged around the

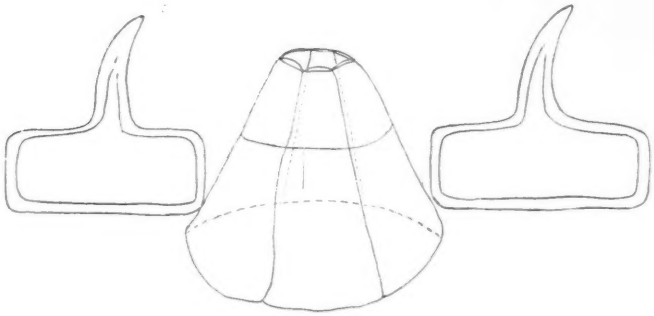


FIG. 2

central stomatal opening. These cells are much thinner-walled than the epidermal cells. In form they are relatively slender distally and broad proximally. As viewed through the microscope, they are darker colored around the stomatal opening and peripherally they are lighter. Since structural material is not available, their exact attitude is made out with difficulty. Their outer centrally directed ends come into focus at about the same time as do the outer ends of the longer spinelike processes, or very soon after, while their inner broad ends are visible after the epidermal cells have gone out of focus; hence it is obvious that they are inclined toward each other and project outward for a considerable distance from beneath the surrounding epidermal cells. It is believed that fig. 2, which is a diagrammatical drawing of a single group of these guard cells and two adjacent epidermal cells viewed in a radial section of a twig, gives an accurate idea of their arrangement and proportions.

In their more essential characters they agree with the stomata as described by ZEILLER for *F. Hoheneggeri* and by VELENOVSKY for *F. bohemica*. Just what were the physiological factors responsible for the great reduction of the leaves and the assumption of the photosynthetic processes by the branches in *Frenelopsis* it is difficult to imagine. Such features are usually associated with peculiarities of climate and habitat, and suggest strong insolation and lack of humidity; but such conditions are not suggested by the other members of the flora associated with *Frenelopsis*, since with the Potomac species are found large numbers of ferns, many of them apparently tree ferns with decompound fronds a meter or more across, and large numbers of cycads of various genera and large size; while in the latest beds in which *F. ramosissima* occurs there are considerable numbers of dicotyledonous leaves, some of which are allied with genera which in the modern flora are confined to tropical areas where the humidity is high and the rainfall heavy.

It is possible that these peculiar features in the cretaceous species of *Frenelopsis* were inherited from triassic ancestors which acquired them during those portions of the Triassic when the climate was extremely arid, as we know it was from physical as well as paleontological criteria.

—EDWARD WILBER BERRY, *The Johns Hopkins University, Baltimore, Md.*

# CURRENT LITERATURE

## BOOK REVIEWS

### The teaching botanist

The second and revised edition of this book[1] is almost completely rewritten and is larger than the former edition by more than 60 per cent. The general plan is quite similar to that of the former book, which was reviewed in this journal eleven years ago (28:276. 1899). During the intervening years attention to the teaching of science has greatly increased; and the author has been a potent factor in stimulating a scientific attitude toward science teaching. Although the results of experiments that have been included in this volume have not furnished solutions to many of the difficult problems, some progress has been made in the direction pointed out in the introduction to the first edition, in which the author said: "The botanical course of the near future must be more adaptive to education, more broad and representative of the science, more economical of energy than in the past."

The book consists of two parts and an appendix. Part one includes nine chapters which deal with the purpose and methods of botanical teaching. It treats of such topics as the place of science in education, the kind of botany that is of most educational worth, desirable characteristics of good teaching and good teachers, the equipment and method of work in the laboratory, botanical books, etc. These discussions are of the greatest value to anyone who teaches botany, and some of the chapters will be found equally helpful to teachers of other sciences. The discussions are broad, free from a didactic attitude, and full of stimulus to new endeavor on the part of those who are engaged in teaching science. The practical suggestions regarding laboratory appliances and the purpose and means of experimentation are almost indispensable to progressive teachers.

Part two consists of "outlines and directions for a synthetic course in the science of botany." It is divided first into the "structure and function of plants," a commendable change from the former titles "the principles of the science of botany," and "natural history and classification of the groups of plants." The order of the topics within these divisions is essentially the same as in the first edition, but the outlines for work are greatly changed. They are more complete and more definite, more easily interpreted by the student, and at the same time better calculated to secure independent investigation and inference. Although the outlines purport to represent a synthetic course,

[1] GANONG, WILLIAM F., The teaching botanist. Revised edition. pp. xi+439. *figs.* 40. New York: Macmillan. 1910.

the morphological, ecological, and physiological treatment of each topic is kept rather distinct. At times excellent work that is suggested in physiology is quite unrelated to the other work with which it appears, as when the physiology of turgidity and osmosis is interpolated under the caption of "the morphology of flowers," or the tropisms under "the morphology of fruits."

There is confessedly presented more work than can be done in a year. The teacher must adjust the course to his needs and facilities. The outline will doubtless prove most valuable in directing many teachers so that they can arrange the kind of course that best suits their needs. An appendix gives the unit statements for courses in secondary schools as they have been outlined by the special committees, one from the Botanical Society of America and the College Entrance Board, and the other from the North Central Association of Colleges and Secondary Schools. These are the two representative organizations that have attempted to outline these statements, and therefore their units should be of particular interest to botanists.

Teachers of botany and botanists in general are greatly indebted to Professor GANONG for this book, which should be influential in enhancing the educational efficiency of science and particularly of botanical science.—O. W. CALDWELL.

### Tropical agriculture

*Agriculture in the tropics* is the title of a book[2] designed to treat chiefly of the commercial aspects of tropical plants, and is in no sense a guide to the practice of agriculture. The most valuable arable lands of the tropics are now under the control of white people, and the book obviously is intended to furnish them with data that "may be helpful and thought-stimulating for the student, administrator, or traveller." The great influence of "western" civilization and agriculture is credited with having brought a revolution in tropical agriculture.

Parts I and II ("The preliminaries to agriculture" and "The principal cultivations of the tropics") will be of interest to students of plant life, while these parts and parts III and IV ("Agriculture in the tropics" and "Agricultural organization and policy") will interest geographers and economists. Topics of special interest in part I are land and soil, climate, drainage and irrigation, and plant life in the tropics (acclimatization). In part II there are presented the leading tropical economic plants and plant products, their botanical nature, history, cultivation, productivity, use, marketability, commercial importance, adaptability to new regions, and dangers from plant and animal parasites. In part III much attention is given to the need of giving modern agricultural education to the peasants who farm the tropical estates.

The book contains an immense amount of statistical matter relative to the

[2] WILLIS, J. C., Agriculture in the tropics; an elementary treatise. pp. xviii+222. *figs. 25*. Cambridge Biological Series. London: Cambridge University Press. $2.50.

importance of agricultural plants and their future possibilities. It will be found a valuable reference book upon many questions pertaining to economic and commercial aspects of tropical plants. Botanically, however, the book is often defective, as for example, in speaking of the growth of *Cannabis sativa* for its opium-like drug, the author says: "The male flowers are removed in November, for if the female flowers are fertilized there is no formation of the drug."—O. W. CALDWELL.

### The geography of ferns

It is a praiseworthy thing for an investigator, who has devoted years to taxonomic exploration, to bring together in readable form the many things of geographic interest which he has observed. It is exactly this service which CHRIST, the well-known student of the ferns, has now performed.[3] The volume is divided into two parts, corresponding somewhat to the usual divisions of ecological and floristic geography. CHRIST regards the ferns as controlled by the same general distributional factors as the seed plants, the most noteworthy difference consisting in the pronounced tendency of ferns to be hygrophytic mesotherms. The great fern areas of the world are essentially coincident with the forest areas, very few species existing where the rainfall is less than 60 cm., and the greatest development occurring where the rainfall is over 200 cm.

The edaphic conditions under which ferns live are first noted, attention being called to the fact that most species are humus forms, and but slightly dependent on the mineral nature of the soil. Under the head of climatic conditions, a number of characteristic fern formations are described. The hygrophytic ferns are treated at considerable length, especial attention being devoted to the epiphytic forms. The features of the xerophytic ferns are well portrayed. In the floristic part of the work, consideration is given to a number of cosmopolites, and also to endemic forms and to species with disconnected areas. The body of the second part is made up of the treatment of the floristic regions of the world. Here, as elsewhere in the volume, the author makes it very clear that the ferns, in spite of their great age, are far from being a senescent group.

The volume is a mine of information, and will be of the highest value to all botanists. The excellent index makes it possible to find at once the known ecological and geographic facts concerning most living ferns.—HENRY C. COWLES.

### An organic chemistry

The third English edition of HOLLEMAN'S *Organic chemistry* has just appeared,[4] edited by A. JAMIESON WALKER. The value of the book as a text

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[3] CHRIST, H., Die Geographie der Farne. 8vo. pp. 358, with frontispiece, *figs. 129* (mostly photographic reproductions), and *3 maps*. Jena: Gustav Fischer. 1910.

[4] HOLLEMAN, A. F., A textbook of organic chemistry. 8vo. pp. xx+599. *figs. 80*. New York: John Wiley & Sons. 1910.

is shown by a statement from the author's preface: "Besides the four editions of the original Dutch volume and three in English, seven editions of this book have been published in German, two in Russian, two in Italian, and one in Polish. A French edition and a Japanese edition are also in preparation.' A second quotation from the preface gives the aim of the book, which is well carried out, and it gives the text its great value as a general reference book' for students of physiology. "Most of the short textbooks of organic chemistry contain a great number of isolated facts; the number of compounds described in them is so considerable as to confuse the beginner. Moreover, the theoretical grounds on which this division of the science is based are often kept in the background; for example, the proofs given of the constitutional formulae frequently leave much to be desired. However useful these books may be for reference, they are often ill-suited for textbooks, as many students have learned from their own experience."

The chapters on sugars, amino acids, and proteins, of the greatest direct interest to physiologists, though brief, are certainly clear statements of the fundamental facts of the chemistry of these bodies. The chapter on proteins is in the body of the book just after amino acids, instead of in an appendix, as it appeared in the second edition. WALKER is credited with having introduced into the book the protein classification adopted by the Chemical Society of London, the English Physiological Society, the American Physiological Society, and the American Society of Biological Chemistry.—WILLIAM CROCKER.

## NOTES FOR STUDENTS

**Magazines for students of genetics.**—The era of experimental study in heredity and evolution has called for new publications devoted to the results of research in this field. While all the biological journals occasionally contain articles which are of interest to the student of experimental evolution, several special magazines have been established which are quite indispensable to anyone who wishes to keep reasonably well informed regarding current progress in genetics and related subjects.

The first of these which deserves mention is *Biometrika*, which was established in London in 1901 under the editorship of Professor KARL PEARSON, for the publication of papers on mathematical methods of dealing with variation, heredity, selection, etc., and the results of their application. While not many of the articles published in *Biometrika* deal strictly with genetics, it was the first journal to voice the demands for more exact methods of investigating problems of evolution, and as the whole trend of modern biology is toward the greater exactness involved in mathematical treatment of biological data, *Biometrika* should continue to fill an increasingly important place, notwithstanding the unfortunate fact that there is a tendency of late to allow personal feeling to dominate both the policy of the magazine and the attitude

of many prominent students of genetics toward it and the methods it advocates.

The second magazine which is devoted specifically to evolution and related subjects is the *Archiv für Rassen- und Gesellschafts-Biologie*, edited and published in München by Dr. A. PLOETZ, assisted by Dr. L. PLATE and several others. This magazine was established in 1904, just at the time when interest in evolution was being revived by the general introduction of the new methods. It is not wholly occupied with the results of experimentation, but contains besides these many philosophical and more or less academic discussions, which give it the flavor of transition from the older evolutionary literature of the post-Darwinian writers to the new type of literature introduced and exemplified by the work of DE VRIES and MENDEL.

In 1908 a new monthly German magazine entitled *Zeitschrift für Induktive Abstammungs- und Vererbungslehre* was established in Berlin under the editorship of Dr. E. BAUR, assisted by Drs. CORRENS, HECKER, STEINMANN, and WETTSTEIN. This magazine is at the present time the most valuable of all similar journals, as it offers in excellent form a large volume of original matter, adequate abstracts from a large proportion of the papers on the same subjects published in other journals, and finally gives a very complete classified list of new literature dealing with the same subjects. This journal is absolutely indispensable to all who wish to investigate problems of heredity, variation, and evolution.

In October 1909 a journal first made its appearance in London entitled the *Mendel Journal*, which is unique in a number of particulars. In the first place, its editorship is entirely anonymous, though many internal evidences leave little doubt as to the source of the dominating influence. It seems to be in a sense the organ of the Mendel Society of London, as it publishes the various addresses made before that body. While this journal has a number of interesting papers which supply valuable data, especially on human inheritance, its whole attitude is one much to be regretted. The express object of the magazine is to furnish a *propaganda* for Mendelism. It represents the "Mendelians" as an army which is fighting an opposing army, the "Biometricians," and makes many unwarranted slurring attacks upon Professor PEARSON and those who have assisted him in working out the biometrical methods of dealing with biological data. No true scientist can fail to deprecate the introduction of propagandism and personal enmity into science. It may be expected that the publication of such a journal will act as a boomerang, and will do the cause of Mendelian investigation a distinct injury. The aim should be simply to arrive at the truth and not to adopt and establish a creed to be forced upon others who cannot be convinced of the truth by the data presented. Like *Biometrika*, the *Mendel Journal* has no regular periodicity, but its appearance is promised whenever sufficient material is at hand.

In America the demand for journals dealing with genetics has brought a most satisfactory response from the *American Naturalist*, which about two

years ago, under the editorship of Dr. J. McK. CATTELL, adopted as a general policy a specialization upon evolutionary topics. The American Society of Naturalists chose for itself the same field, and the *American Naturalist* is in a certain sense the organ of that society.

The last arrival in the field is the new magazine issued by the American Breeders' Association, and known as the *American Breeders' Magazine*, published in Washington under the editorship of the secretary of the Association, W. M. HAYS, assisted by the secretaries of the Plant and Animal Sections, N. E. HANSEN and H. W. MUMFORD. The first issue of this magazine has just appeared, and gives every evidence of its intention to take a dignified place among economic journals, and a modest and unassuming place among scientific magazines, thus correctly representing the unique position of the Association whose organ it is. The *American Breeders' Magazine* is being issued as a quarterly, but it is hoped by those who have it in charge that it may soon be changed to a monthly magazine. The opening number presents as a frontispiece a portrait of CHARLES DARWIN, and also gives portraits of GREGOR MENDEL and AMOS CRUIKSHANK, the latter the originator of the shorthorn cattle, and said to be the first to utilize fully the discovery of a mutation in the establishing of an important economic breed. Besides brief biographical sketches of these three men, this first issue presents papers on "Increasing protein or fat in corn," by L. H. SMITH; "New methods of plant-breeding," by GEORGE W. OLIVER; "The army horse," by CARLOS GUERRERO; "Imperfection of dominance," by C. B. DAVENPORT; "Poultry-breeding in South Australia," by D. F. LOWREY; and several articles on the breeding of deer and other wild animals by D. E. LANCE and other members of the committee on breeding wild animals. As it is the plan of the American Breeders' Association to continue the publication of its *Year Book*, the issue of this magazine will make it even more important that all those who are engaged in investigation or who are interested in matters involving genetics should become members of the Association and thus secure its publications.—GEO. H. SHULL.

**Respiration.**—PALLADIN[5] has tested the effect of several poisons on the $CO_2$ output from living plant organs and from similar tissues that have been killed by freezing for several hours. He finds that 0.09 per cent quinine hydrogen chlorid more than triples the $CO_2$ output from living stem tips of *Vicia Faba*, while it does not affect the killed ones; 0.05 per cent was far less effective on the living tissue and indifferent in the dead; and 1.0 per cent tripled the product from the living and reduced it markedly in the dead tissue. In the living bulbs of *Gladiolus Lemonia*, 8 cc. of ether per 7.5 liters of air

[5] PALLADIN, W., Ueber die Wirkung von Giften auf die Atmung lebender und abgetöteter Pflanzen, sowie auf Atmungenzyme. Jahrb. Wiss. Bot. 47:431–461. 1910.

doubled the $CO_2$ production, while 16 cc. in the same volume was less effective. Neither increased the output from killed bulbs. Ether gave little stimulation in the living bulbs of *Gladiolus Colvillii* and *Allium Cepa*, while it cut greatly the output from dead tissues. Arbutin (1 and 2 per cent) reduced considerably the $CO_2$ yield from live wheat seedlings, and very markedly that from killed ones. PALLADIN finds that the stimulative or inhibitory effect of poisons on the living tissues was not accompanied by an increase or decrease in peroxidase, but the decreased output from dead tissues was accompanied by a decrease in peroxidase. The stimulatory effect of poisons gradually disappears and toxic results soon set in if the surrounding atmosphere is displaced by hydrogen. Extreme temperatures also reverse the effect of the poisons. The author believes that the increased $CO_2$ output in the living tissues is a result of their battling against the poison, and that the ability to do battle is lost with death or with unfavorable life conditions. He concludes that the action of poisons on the respiration of dead tissues is a direct result of injury to the respiratory enzymes, while their action on living plants is indirect through the living protoplasm.

PALLADIN believes that the increased respiration is due to an increased transformation of the zymogens to active enzymes, which is also accompanied by an increased destruction of the active enzymes. For this reason the stimulated plant shows no increase in active enzymes over the control. One feels that this conclusion is not sufficiently backed by evidence.

PALLADIN[6] has also attempted to ascertain the effect of contained lipoids upon the respiration of plant tissues. This he did by extracting dried wheat seedlings for two hours with various lipoid solvents (toluol acetone, benzen, chloroform, benzin, alcohol, etc.). In general he finds that the more lipoid and therefore phosphorus-containing material the solvent extracts, the more it reduces respiration. He believes this is related to the important rôle of phosphates in zymase action. He finds, however, that the amount of reduction in respiration is not exactly proportional to the amount of lipoid extracted. He explains this in part by the fact that different solvents will extract not only different amounts, but different sorts of lipoids. In substance he also says: "When we separate the lipoids we destroy the normal protoplasmic structure. We separate from the protoplasm the cement which binds its heterogeneous parts into a whole. I have shown that even the mechanical breaking up of the plasma structure reduces very markedly the respiration of the plant tissue." He points out various other means through which these solvents may affect the respiration, such as the coagulation by alcohol. With other authors, he believes the lipoids are to be considered intermediary bodies in respiration, that is, oxygen-carriers. He would list them with his respiratory chromogens. One gets the impression that PALLADIN feels himself much more secure than he should when treading on such uncertain ground.

[6] PALLADIN, W., Zur Physiologie der Lipoide. Ber. Deutsch. Bot. Gesell. 28:120–125. 1910.

GALITZKY and WASSILJEFF[7] have studied the effect of boiled extract of wheat and bean seeds upon the respiration of living and killed (by treatment with acetone) wheat seedlings. In agreement with various other workers, they find that the extracts greatly increase the $CO_2$ output in both living and killed seedlings: 60 per cent in normally acid cultures, 117 per cent in neutral cultures, and 86 per cent in slightly alkaline cultures. The authors raise the question, "Is the stimulative action due to food materials supplied by the extract, or to bodies of the nature of co-enzymes?" L. and N. IWANOFF have assumed that the stimulation is due to the action of organic or inorganic phosphates on anaerobic respiration, analogous to the action of these bodies as co-enzymes for zymase. The authors find that peptone, glycerin, mannit, sodium lactate, quinic acid, sodium chlorid, and ferric chlorid have very little or no effect upon the respiration of the seedlings. Dextrose, saccharose, maltose, and sodium carbonate give a slightly increased $CO_2$ output, about 20 per cent. Arabinose and ferrous sulfate give a somewhat greater stimulation of the extracts. The authors consider it especially interesting that probable intermediate products of alcoholic fermentation, lactic acid and sodium lactate, have no stimulative effect. This is quite in contrast with conceptions of KOSTYTSCHEW. The authors are to extend the tests to various other substances, especially to phosphates, to see whether they will give the amount of stimulation shown by the extracts. One naturally wonders to what extent bacterial action may increase the $CO_2$ output. So far as methods are described, one certainly cannot be assured that such has not happened.—WILLIAM CROCKER.

**Heliotropism and geotropism.**—GUTTENBERG[8] has already shown, contrary to the earlier conception of most writers, that the effect of the geotropic stimulus is not annulled by the light stimulus, but that light of such intensity can be chosen that, when it strikes a horizontally placed orthotropic epicotyl from below, its joint action with gravity will, after various nutations, lead to the epicotyl permanently growing in the horizontal position. Compensation (placement at 45 above the horizontal) likewise results when the light of proper intensity strikes the vertical epicotyl horizontally. The intensity of light demanded to compensate gravity varies greatly with different epicotyls; while occasionally greater than one candle power, it is generally only a fraction of a candle power. RICHTER[9] called the results of GUTTENBERG into question,

[7] GALITZKY, KATHERINE, und WASSILJEFF, VERA, Zur Atmung der Weizenkeime. Ber. Deutsch. Bot. Gesell. **28**:182–187. 1910.

[8] GUTTENBERG, H. R. v. Ueber das Zusammenwirken von Heliotropismus und Geotropismus in parallelotropen Pflanzenteilen. Jahrb. Wiss. Bot. **45**:193–231. 1907.

[9] RICHTER, O., Ueber das Zusammenwirken von Heliotropismus und Geotropismus. Jahrb. Wiss. Bot. **46**:481–502. 1909.

maintaining that the results were modified by the gaseous impurities of the laboratory in which they were obtained. GUTTENBERG,[10] on repeating his experiments in pure air, finds essentially the same compensatory values of light as he found in his earlier work. GUTTENBERG used the seedlings of *Avena* and *Brassica*, forms much less sensitive to impurities than are legumes, with which RICHTER worked. GUTTENBERG finds in *Vicia sativa*, contrary to RICHTER, that laboratory air does not increase the heliotropic sensitiveness, but in agreement with RICHTER he finds the geotropic irritability lessened. On this point, GUTTENBERG'S experiments are much more critical than RICHTER'S.—WILLIAM CROCKER.

**Morphology of Phylloglossum.**—A recent paper by WERNHAM[11] represent, a type, at the moment becoming much too common, in which a small basis of imperfectly examined facts is made to serve for large conclusions which are neither clearly nor logically drawn. The author has examined by means of serial sections the anatomy of two specimens of *Phylloglossum Drummondii*. He concludes that the basal leaves of this species (the protophylls of certain authors) are microphyllous, although superficially relatively large in sizes because their traces leave the stele without leaving any gap, as is the case with the Lycopsida. Concerning the relation of the sporophyll traces to the vascular system of the axis, the account is very obscure, since it is not made clear whether gaps are or are not present. The most remarkable feature of the article is the interpretation of the larger strand which passes off from the crown of the functional tuber toward the tuber of the succeeding year as a leaf trace. It has been regarded by other observers, apparently with good reason, as a branch supply, and the present author adduces apparently no valid evidence why this view of its nature should not continue to be held. On the basis of this imaginative interpretation, he comes to the conclusion that *Phylloglossum* was originally a megaphyllous form, which has become much reduced. It would be possible to prove almost anything with such reasoning as this. It seems highly desirable that morphologists should avoid eccentric conclusions of the nature illustrated by the article here reviewed. Obviously, conclusions of permanent value in regard to leaves or other organs can be reached only in the case where there is no room for doubt as to the morphological category of the structure under discussion.—E. C. JEFFREY.

**Classification of conifers.**—A new classification of conifers, based upon morphology, geographical distribution, and geological history, is proposed

[10] GUTTENBERG, H. R. v., Ueber das Zusammenwirken von Geotropismus und Heliotropismus und die tropistische Empfindlichkeit in reiner und unreiner Luft. Jahrb. Wiss. Bot. **37**:467–492. 1910.

[11] WERNHAM, H. F., The morphology of *Phylloglossum Drummondii*. Annals of Botany **24**:335–347. *figs. 8*. 1910.

by VIERHAPPER.[12] It is assumed at the outset that a group whose members have in common such striking characters must be monophyletic. The morphology is confined to the grosser taxonomic characters (but includes the structure of the wood), excluding entirely the gametophytic structures, because the new system is based upon facts, and the gametophytes are not yet known in all the genera, and presumably are not yet worthy of recognition among the established facts. The obvious characters are analyzed and classified as primitive and secondary.

The Cordaitinae are the primitive stock, which during the Carboniferous gave rise to the Coniferae, the Taxocupressaceae arising as an offshoot from Ginkgoinae, and the Abietaceae coming directly from the Cordaitinae. The Taxocupressaceae include the Taxoideae and Taxodioideae arising independently from the *Ginkgo* stock during the Carboniferous, and the Cupressoideae arising during the Trias from the Taxodioideae. The Abietaceae include the Araucarioideae coming directly from the *Cordaites* stock, and the Cunninghamioideae and Abietoideae arising from the araucarian stock during the Trias.

Without commenting upon the scheme itself, it would seem to the reviewer that so much is now known about the gametophytes, and that so much of this comparatively recent knowledge is extremely significant, that it must be considered in any classification which claims to represent the phylogeny of a group.—CHARLES J. CHAMBERLAIN.

**Cretaceous pine leaves.**—In the communication cited the authors describe the anatomy of a species of *Pinus* and a supposed species of *Prepinus*, from the Upper Cretaceous of Hokkaido, Japan.[13] The pine leaf, denoted by the specific name *P. yezoensis*, from the description given is not very different in structure from the living *P. Bungeana* of China, since it is a soft pine with a single foliar bundle and apparently a three-leaved fascicle. In type it clearly differs from the pine leaves of the Lower Cretaceous described by the reviewer, in possessing a degenerate transfusion sheath, a well-marked endodermis, and infolded mesophyll cells. In other words, it is practically indistinguishable in its general structure from the leaf of a living pine. Interestingly enough, in a communication from the reviewer's laboratory, shortly to appear, it will be shown that the wood of a pine from the American Upper Cretaceous likewise resembles more nearly the secondary xylem of living pines than that of pines from the Lower Cretaceous. It will thus apparently be possible to distinguish between these two horizons by means of the nature of the pine flora. The *Prepinus* described, *P. japonicus* (why not *P. japonica?*), appar-

[12] VIERHAPPER, F., Entwurf eines neuen Systemes der Coniferen. Abhandl. K. K. Zool.-Bot. Gesell. Wien **5**:1–56. 1910.

[13] STOPES, MARIE C., and KERSHAW, E. M., The anatomy of cretaceous pine leaves. Annals of Botany **24**:395–402. *pls. 27, 28.* 1910.

ently does not belong to that genus at all, since it is without the very striking internal transfusion sheath of the lower cretaceous genus, has a double instead of a single foliar bundle (a point of great importance, as will be recognized by those versed in the anatomy of *Pinus* in its living species), and no centripetal xylem. The authors make light of the absence of the last feature, but in this they are apparently not well advised.—E. C. JEFFREY.

**Conduction of stimulus.**—ROTHERT has shown that the conduction of stimulus of unilateral illumination from the tip of the *Avena* seedling to the darkened basal portion occurs when the vascular strands are cut; and that a horizontal incision on one side, whether toward, away, or on the flank in reference to the one-sided illumination, still permits conduction. FITTING showed that when the incision was away from the light and a mica plate inserted, no conduction occurred. The insertion of a slice of rattan in the same position did not prevent conduction; the latter of course allows the continuity of water and solution. When the mica plate was inserted in an incision on the lighted side, conduction was not hindered. JENSEN[14] finds that with the incision away from the light, no conduction occurs in dry air or in water. He assumes that under favorable conditions the stimulus can be conducted across the wound while under unfavorable conditions it cannot. In saturated air the stimulus was also conducted from the tip to the darkened base, even after the tip (1 cm. long) had been entirely cut off and set back and fastened by gelatin and cocoa butter.—WILLIAM CROCKER.

**Embryo sac of Pandanus.**—In 1909 CAMPBELL published an account of the embryo sac of *Pandanus*, which was reviewed in this journal (**47**:485, 1909). In this Javanese material the fertilization stage was not secured, so that it was not certain that the interesting situation described is the one at fertilization. Now there has come to hand additional material (*P. coronatus*) which has supplied the missing stage.[15] An ordinary egg apparatus is organized, but there occurs "a large discoidal mass of cells" at the antipodal end of the sac, and fusions of "polar" nuclei (up to six) were observed. The number of cells in the sac at the fertilization stage would thus seem to be greater than that recorded for any other angiosperm. The amount of antipodal tissue suggests the situation in *Sparganium*, the difference being that in the latter genus this tissue develops after fertilization.—J. M. C.

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[14] JENSEN, P. BOYSEN, Ueber die Leitung des phototropischen Reizes in Avenakumpflanzen. Ber. Bot. Gesell. **28**:118–120. 1910.

[15] CAMPBELL, DOUGLAS H., The embryo sac of *Pandanus coronatus*. Bull. Torr. Bot. Club **24**:293–295. *figs. 6.* 1910.